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## THE PAST, PRESENT AND FUTURE WATER SUPPLY OF LONDON.<sup>1</sup>

IN a discourse to the Members of the Royal Institution on the subject of the Metropolitan Water Supply nearly thirty years ago, I stated that out of every thousand people existing upon this planet at that moment, three lived in London; and, as the population of London has in the meantime doubtless grown at a more rapid rate than that of the rest of the world, it will probably be no exaggeration to say that now, out of every thousand people alive on this earth, four live in London; and therefore any matter which immediately concerns the health and comfort of this vast mass of humanity may well merit our most earnest attention. Amongst such matters that of the supply, in sufficient quantity, of palatable and wholesome water is certainly not the least in importance.

It is not therefore surprising that this subject has received much attention from several Royal Commissions,—notably from the Royal Commission on Water Supply of 1867, presided over by the Duke of Richmond, the Royal Commission on the Pollution of Rivers and Domestic Water Supply of Great Britain, presided over by the late Sir William Dennison, of which I had the honour to be a member; and lastly the Royal Commission, appointed in 1892 to inquire into the Water Supply of the Metropolis,

<sup>1</sup> A discourse delivered at the Royal Institution, 21st February, 1896.

of which Lord Balfour of Burleigh was Chairman, and of which Professor Dewar was a member.

The Royal Institution has also for nearly three-quarters of a century been prominently connected with the investigation and improvement of the Metropolitan Water Supply ; no less than four of our Professors of Chemistry having been successively engaged in this work, *viz.*, Professors Brande, Odling, Dewar, and myself, whilst three of them have been members of the Royal Commissions just mentioned. I may therefore perhaps be excused for accepting the invitation of our Secretary to bring the subject under your notice for the third time.

On the present occasion I propose to consider it from three points of view, *viz.*, the past, the present and the future ; and, for reasons which will appear hereafter, I shall divide the past from the present at, or about, the year 1883, and will not go back farther than the year 1828, when Dr. Brande, Professor of Chemistry in the Royal Institution ; Mr. Telford, the celebrated engineer ; and Dr. Roget, Secretary of the Royal Society were appointed a Royal Commission to inquire into the quality and salubrity of the water supplied to the Metropolis.

The Commissioners made careful examinations and analyses, and reported as follows : "We are of opinion that the present state of the supply of water to the Metropolis is susceptible of, and requires, improvement ; that many of the complaints respecting the quality of the water are well founded, and that it ought to be derived from other sources than those now resorted to, and guarded by such restrictions as shall at all times ensure its cleanliness and purity. (At this time the water was pumped from the Thames between London Bridge and Battersea.) To obtain an effective supply of clear water free from *insects* and all suspended matter, we have taken into consideration various plans of filtering the river water through beds of sand and other materials ; and considering this, on many accounts, as a very important object, we are glad to find that it is perfectly possible to filter the whole supply, and this within such limits, in point of expense, as that no serious objection can

be urged against the plan on that score; and with such rapidity as not to interfere with the regularity of service."

*Before the year 1829*, therefore, the river water supplied to London was not filtered at all; but after the issue of this report, the Companies set themselves earnestly to work to improve the quality of the water by filtration.

The first filter, on a working scale, was constructed and brought into use by the Chelsea Water Company in the year 1829. But even as late as 1850 only three out of the seven principal companies filtered the river water which they delivered in London; and it was not until 1856 that filtration was made compulsory by Act of Parliament, whilst it can scarcely be doubted that, between this date and the year 1868, when my observations on turbidity were first commenced, the operation was very imperfectly performed.

In the year 1832, and again in 1849, London was severely visited by epidemic cholera, and the agency of drinking water in spreading the disease forced itself upon the attention of the observant portion of the medical profession. It was Dr. Snowe, however, who in August, 1849, first formally enunciated the doctrine that drinking water polluted by choleraic matters is the chief mode by which cholera is propagated.

Received at first with incredulity, this doctrine was supported by numerous facts, and it soon caused renewed attention to be directed to the quality of the water then being supplied to the Metropolis; with the result that the intakes of the various Companies drawing from rivers were, one after another, removed to positions above the reach of tidal influence; the Thames water being withdrawn from the river above Teddington Lock, and the Lea water at Ponder's End, above the tidal reaches of that river.

In every visitation of Asiatic cholera to London, the water supply was either altogether unfiltered or imperfectly filtered, besides being derived from highly polluted parts of the Thames and Lea; and the enormous loss of life, amounting in the aggregate to nearly 36,000 people, can only be attributed to this cause. It has been abundantly proved that efficient filtration is a perfect safeguard against

the propagation of the disease, and since the year 1854 no case of Asiatic cholera in London has been traced to the use of *filtered* river water.

These are the results arrived at by the most general investigation of the subject. They show that in every epidemic, the mortality varied directly with the intensity of the drainage pollution of the water drunk by the people ; but if time permitted, a more detailed study of the statistics in both epidemics would demonstrate, much more conclusively, this connection between cholera mortality and the pollution of drinking water—a connection which has quite recently been terribly emphasised in the case of Hamburg.

Such is the verdict with regard to *cholera*, and the same is true of that other great water-borne disease *typhoid fever*. But, unlike cholera, this disease is disseminated in several other ways, and its presence or absence in any locality may not, of necessity, have any connection with drinking water, as is strikingly shown by the health statistics of Manchester.

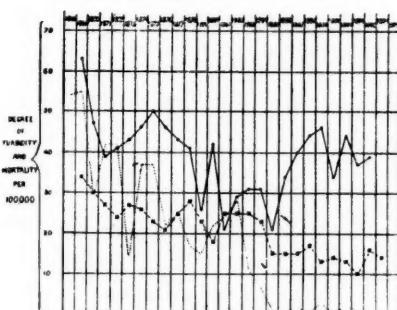
There is no evidence whatever that, since the year 1869, when typhoid fever appeared for the first time as a separate disease in the Registrar General's reports, it has been conveyed by the water supply of the Metropolis. An inspection of the diagram (No. 1) shows, it is true, a greater proportional mortality during the period of imperfect filtration than during the later period ; that is to say from 1883 when the process began to be performed with uniform efficiency ; but the plotting of a similar curve for the deaths by typhoid in Manchester shows that this disease arises from other causes than polluted water, since the water supply of Manchester, derived as it is from mountain sources, is above all suspicion of this kind. These other causes have during the last ten years been much mitigated in London by various sanitary improvements ; whilst, as shown in the diagram, there has been no corresponding mitigation in Manchester.

Although very soon after the year 1856 all the water supplied to the Metropolis was obtained from sources much less exposed to drainage pollution, it was still very carelessly

filtered. Previous to the year 1868, there are no records of the efficiency, or otherwise, of the filtration of the Metropolitan water supply derived from rivers, as distinguished from deep wells, the water of which is perfectly clear without filtration.

It was in the year 1868 that I first began to examine the water supplied to the Metropolis from rivers *with reference to efficiency of filtration*. In that year, out of eighty-four samples examined, seven were very turbid, eight turbid, and ten slightly turbid, so that altogether no less than nearly 30 per cent. of the samples were those of *inefficiently* filtered water. The Metropolitan Water Supply then, up to the year 1868, may be shortly described as

TYPHOID IN LONDON AND MANCHESTER CONTRASTED WITH TURBIDITY.



No. 1.

derived for many years from very impure sources with either no filtration at all, or with very inefficient filtration; and afterwards, when the very impure sources were abandoned, the supply was still often delivered in a very inefficiently filtered condition. But, after the establishment of monthly reports on the filtration of the river-derived supplies, the quality of these waters gradually improved in this most important respect, as is seen from diagram No. 1. In this diagram, the continuous line with dots represents the mortality from typhoid in Manchester, the broken and eroped line the contemporaneous mortality in London, and the dotted curve the degree of turbidity of the London water supply.

These observations graphically represented in the diagram show that, at the time they were commenced, the filtering operations were carried on with considerable carelessness, and that this continued, though to a less extent, down to the year 1883, since which time, and especially since 1884, the efficiency of filtration of all the river waters supplied to the Metropolis has left little to be desired.

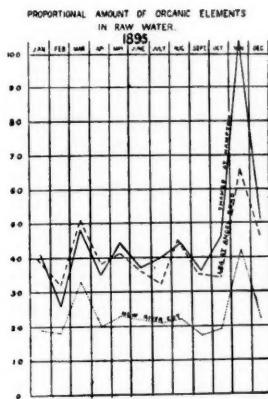
What is it then that separates the *past* from the *present* water supply of London? In the first place there is the change of source—I mean the change in position of the intakes of the several Companies drawing from the Thames and Lea—and the total abandonment of the much-polluted river Ravensbourne by the Kent Water Company. So long as the water supply was derived from the tidal reaches of the Thames and Lea, receiving as these reaches did the drainage of immense populations, the risk of infection from water-borne pathogenic organisms could scarcely be otherwise than imminent; for, although we now know efficient filtration to be a perfect safeguard, anything short of efficiency must be attended with risk in the presence of such extreme pollution.

Nevertheless, the line of demarcation between the past and the present water supply of the Metropolis is, in my opinion, to be drawn, not when the intakes of the river companies were removed to positions beyond the possibility of pollution by the drainage of London, but it must be drawn at the time when *efficient filtration* was finally secured and ever since maintained, that is to say, in the year 1884.

The removal of turbidity by sand filtration, however, refers only to suspended matters; but there are sometimes objectionable substances in solution of which organic matter is the most important. River water and mountain water, even when efficiently filtrated, contains more organic matter than spring or deep well water; but this is reduced in quantity by storage and especially by filtration, although these waters can perhaps never be brought up to the standard of organic purity of spring and deep well water.

## THE PRESENT WATER SUPPLY.

At present London is supplied with water from four sources—the Thames, the Lea, the New River, and deep wells. Of these the deep wells yield as a rule the purest water, requiring no filtration or treatment of any kind before delivery for domestic use. The river waters, on the other hand, require some kind of treatment before delivery—storage, subsidence in reservoirs, and filtration. The water from the Thames is abstracted at and beyond Hampton, far above the reach of the tide and London drainage. The water from the Lea is taken out at two points, *viz.*, at Angel Road near Chingford, by the East London Water Company,

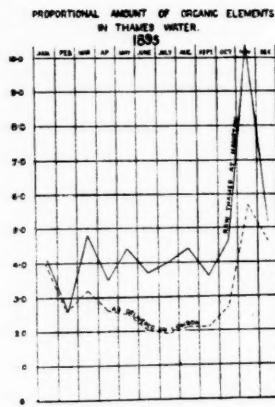


No. 2.

and above Hertford by the New River Company, who convey it to Green Lanes by an open conduit twenty-five miles long, called the New River Cut, in which it is mixed with a considerable volume of spring and deep well water.

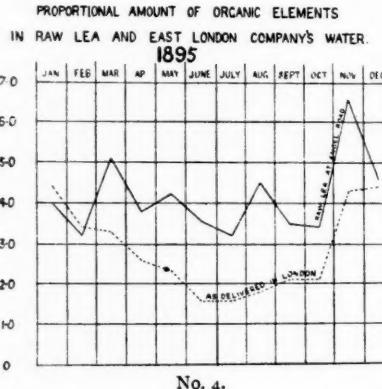
All three river waters are affected by floods and are, as raw materials, of considerably different quality as regards organic purity (see diagram No. 2). From these raw materials by far the largest volume of the Metropolitan Water Supply is derived, and the chemical or organic purity of the water sent out to consumers stands in direct relation to the organic purity of the raw material used, as

is seen from the diagrams Nos. 3, 4 and 5, which show the proportional amounts of organic elements in the raw and filtered waters; they also show the advantage of storage in excluding flood water, No. 4 shows that floods in March



No. 3.

and August were circumvented, but not in November. The numbers in the margins of the diagrams express the proportional amount of organic elements, that in the Kent



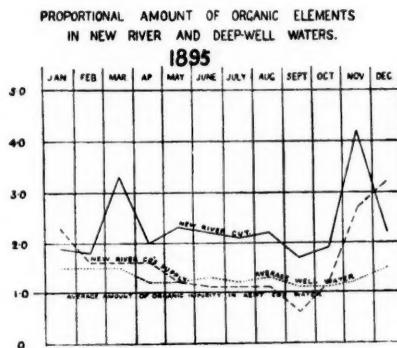
No. 4.

Company's water during the nine years ending December 1876 being taken as unity, as is depicted in diagram No. 5.

Hitherto I have spoken of *chemical* purity or comparative freedom from organic matter only, but the spread of diseases

such as cholera and typhoid fever through the agency of drinking water has no connection whatever with the chemical or organic purity of the water. These diseases are propagated by living organisms of extreme minuteness, to which the names bacilli, bacteria, and microbes have been given, and here comes the important question how, if at all, does filtration secure immunity from these water-borne diseases?

To Dr. Koch of Berlin, we are indebted for the answer to this question. By his discovery of a means of isolating and counting the number of bacteria, or bacilli, or microbes and their spores in a given volume of water, we were, for the first time, put into possession of a method by which the condition of water as regards these living organisms, before



No. 5.

and after filtration, can be determined with quantitative exactness. The enormous importance of this invention (which was first made known and practised in England in 1882 by the late Dr. Angus Smith) is evident, when it is borne in mind that the living organisms, harmful or harmless, contained in water are of such extreme minuteness as practically to defy detection by ordinary microscopical examination. But although the microscope cannot detect with certainty single bacteria or their spores, even the naked eye can easily discern *towns* or *colonies* consisting of thousands or even millions of such inhabitants.

Dr. Koch's method accomplishes at once two things: it isolates, in the first place, each individual microbe or

germ ; and, secondly, places it in conditions favourable for its multiplication which takes place with such amazing rapidity that, even in a few hours, or at most in two or three days, each organism will have created around itself a visible colony of innumerable members—a town in fact comparable to London itself for population.

By operating upon a known volume of water, such as a cubic centimetre for instance, the number of separate organisms or their spores, in a given volume of the water under investigation can thus be determined. The following is the method now adopted in carrying out Koch's process for the bacterial investigation of drinking water :—

1. Preparation of the nutritive medium.
2. Sterilisation of the medium.
3. Collection of the sample of water in a vacuous tube afterwards to be hermetically sealed.
4. Transport of the sample to the bacteriological laboratory, *packed in ice* to prevent multiplication.
5. Mixture of a known volume of the water sample with the nutrient medium.
6. Casting of the mixture into a solid plate.
7. Incubation of the solid plate.
8. Counting of the colonies.
9. Examination of separate colonies, or rather of the individual members under the microscope.

Sometimes the cultivations are made upon a plate of the substance called *agar* which resembles isinglass, and bears a temperature of blood heat without melting.

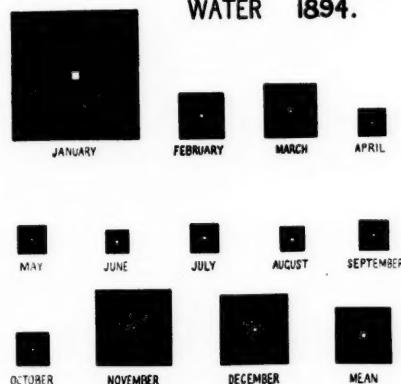
In order to ascertain the effect of filtration upon the bacterial quality of water, it is absolutely necessary that the sample should be taken immediately after it has passed through the filters ; for, if it be obtained from the delivery mains in town, that is to say, after the water has passed through many miles of pipes, the rapid multiplication of these organisms, except in very cold weather is such, that a water which contains only a single living organism per cubic centimetre, as it issues from the filter, may contain

100 or 1000 in the same volume when, after several hours, it arrives on the consumer's premises.

Now what is the effect of sand filtration as carried out by the various Water Companies supplying London upon the living matter contained in the raw river water? *It is simply astounding*: water containing thousands of bacteria per cubic centimetre, for a single drop of Thames water sometimes contains nearly 3000 separate living organisms, comes out from the sand filters with fifty, thirty, ten, or even less of these organisms per cubic centimetre, or the number of microbes in a single drop is reduced to two or even to zero.

MICROBES IN RAW AND FILTERED THAMES

WATER 1894.



No. 6.

Rather less than one-tenth of the total volume of water supplied to London is derived by the Kent Water Company from deep wells in the chalk. As it issues from the porous rock into the fissures and headings of these wells, this water is, in all probability, absolutely sterile; but by the time it has been pumped up to the surface it usually contains a certain number, though small, of microbes. Thus, during the year 1892 it contained on the average six per cubic centimetre in 1893, thirteen; in 1894, fifteen; and in 1895, eight.

The diagram No. 6 shows graphically the bacterial improvement of the Thames water by filtration during

the year 1894. In this diagram the black squares represent the number of microbes in a given volume of the raw water in each month, and the white centres the number remaining in the same volume after filtration.

Although deep well water has, from a bacterial point of view, a decided advantage, the filtered river waters are not very far behind, and there is every reason to believe that with the improvements which are now being carried out by the various river Water Companies, the Kent Company's deep well water will, before long, be run very hard by the other supplies.

By the examination of the water as it issues from the filters, the utmost freedom from microbes, or maximum degree of sterility of each sample is determined. This utmost freedom from bacterial life after all sources of contamination have been passed is obviously the most important moment in the history of the water; for the smaller the number of microbes found in a given volume at that moment the less is the probability of pathogenic or harmful organisms being present; and although the non-pathogenic may afterwards multiply indefinitely this is of no consequence in the primary absence of the pathogenic; but it is only fair, in describing the character of the present water supply of London, to say that not a single pathogenic organism has ever been discovered even in the *unfiltered* water as it enters the intakes of the various Companies, although these organisms have been carefully sought for. It is sometimes said that the non-pathogenic organisms found in water *may* be beneficial to man; but this idea is not borne out by the fact of their entire absence from the food which nature provides for young animals. Healthy milk is absolutely sterile.

As it is at present impracticable to obtain water, uniformly at least, free from microbes, it is desirable to adopt some standard of bacterial purity; and 100 microbes per cubic centimetre has been fixed upon by Dr. Koch and myself as the maximum number allowable in potable water. This standard is very rarely infringed by the London Water Companies, whilst I have every reason to hope that,

in the near future, now that special attention is directed to bacterial filtration, it will not be approached within 50 per cent. This hope is based not only upon my own observations, but also upon the exhaustive and exceedingly important investigations carried out at the Lawrence Experiment Station by the State Board of Health of Massachusetts, under the direction of Mr. George W. Fuller, the official biologist to the Board.

More than six years have already been spent in the prosecution of these American experiments, and many thousands of samples of water have been submitted to bacterial cultivation. The Massachusetts experimental filters are worked at rates up to 3,000,000 gallons per acre daily, which renders the results available for application to public water supplies; indeed none of the water delivered in London is filtered at so rapid a rate as this. It was found that at these rates all the disease-producing germs, which were intentionally and in large numbers added to the unfiltered water, were substantially removed. The filters were so constructed and arranged as to allow direct comparison of the bacterial purification of water under different rates of filtration, with sand of different degrees of fineness, with different depths of the same sand, and with intermittent and continuous filtration.

The actual efficiency of these filters was also tested by the application of the bacillus of typhoid fever. Very large numbers of these bacilli and of other species were applied in single doses to the several filters at different times, and the effluent was examined four times daily for several days afterwards. The results so obtained give a thoroughly trustworthy test of the degree of bacterial purification effected by each of the experimental filters, and these are the data which have been largely used by the Massachusetts State Board of Health in deducing the rules which they consider ought to be observed in water filtration.

Among the subjects investigated by means of these experimental filters were:—

1. The effect, upon bacterial purification, of the rate of filtration.

2. The effect of size of sand grains upon bacterial purification.
3. The effect of depth of material upon bacterial purification.
4. The effect of scraping the filters upon bacterial purification.

Time does not permit of my giving the answers to these questions in detail; but they may be summarised as follows:—

1. The rate of filtration between 500,000 and 3,000,000 gallons per acre per day exercises practically no effect on the bacterial purity of the filtered water. It is worthy of note that the rates of filtration practised by the several Water Companies drawing their supplies from the Thames and Lea are as follows: Chelsea Company, 1,830,000; West Middlesex, 1,359,072; Southwark Company, 1,568,160; Grand Junction Company, 1,986,336; Lambeth Company, 1,477,688; New River Company, 1,881,792; and East London Company, 1,393,920. Hence not one of the London Companies filters at the rate of 2,000,000 gallons per acre per day; at which rate in the Massachusett's filters 99·9 per cent. of the microbes present in the raw water were removed.

2. The effect of size of sand grains was found to be very considerable; and, in confirmation, I find that by the use of a finer sand than that employed by the Chelsea Company, the West Middlesex Company is able, with much less storage, to attain an equal degree of bacterial efficiency.

3. The depth of sand, between the limits of one and five feet, exercises no practical effect on bacterial purity when the rate of filtration is kept within the limits just specified. And this result is quite borne out by my own experience gained in the bacterioscopic examination of the filtered waters of the seven Companies supplying the Metropolis from rivers. Thus the New River Company, with 1·8 feet of sand on the filters, compares favourably with the Chelsea Company, the sand on whose filters is more than twice that depth.

Placed in the order of thickness of sand on their filters, the Metropolitan Companies range as follows: Chelsea,

Lambeth, West Middlesex, Southwark, East London, Grand Junction, and New River. Placed in the order of efficient filtration they range as follows: Chelsea and West Middlesex equal, New River, Lambeth, East London, Southwark, and Grand Junction.

4. When there is such an accumulation of deposit on the surface of a sand filter that, for practical purposes, sufficient water cannot be made to pass through it, the surface of the filter has to be scraped; that is to say, the mud and about half an inch of the sand are removed from the surface. After this operation, there is sometimes an increase in the number of bacteria in the filtered water, and it was noticed that the increase was greater in shallow than in deep filters and with high than with low rates of filtration; and there is no doubt that the effect of scraping is considerably magnified when coarser descriptions of sand are employed, as in the case of the filters of the London Water Companies. I should like, therefore, to impress upon the engineers of these Companies the desirability of using finer sands than are at present employed.

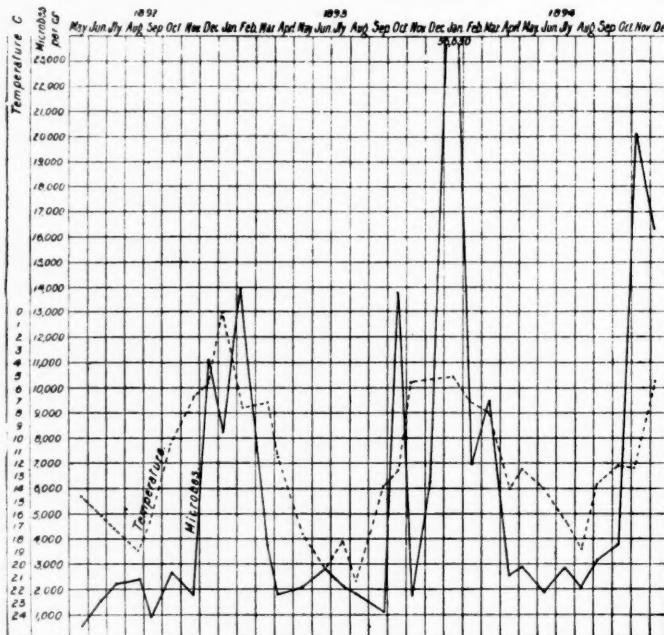
#### INFLUENCE OF THE BACTERIAL CONDITION OF THE RAW RIVER WATER UPON THAT OF THE FILTERED EF-FLUENT.

I have found that the number of bacteria in a given volume of filtered water is to a considerable extent influenced by the number contained in the raw water supplying the filter; and from this point of view, therefore, the bacterial condition of the raw river water used in the Metropolis is of no inconsiderable importance.

Since May, 1892, I have made monthly determinations of the number of microbes capable of developing on a gelatine plate in a given volume of raw Thames water collected at the intakes of the Metropolitan Water Companies at Hampton; and the number has varied during this time between 631 and 56,630 per cubic centimetre, the highest numbers having, as a rule, been found in winter or when

the temperature of the water was low, and the lowest in summer or when the temperature was high.

Now, besides temperature, there are two other conditions to either of which this difference may be attributed, *viz.*, sunshine and rainfall, and I have endeavoured by a series of graphic representations to disentangle these possible influences from each other by placing the results of the microbe determinations in juxtaposition with (1) the temperature of the water at the time the samples were taken;

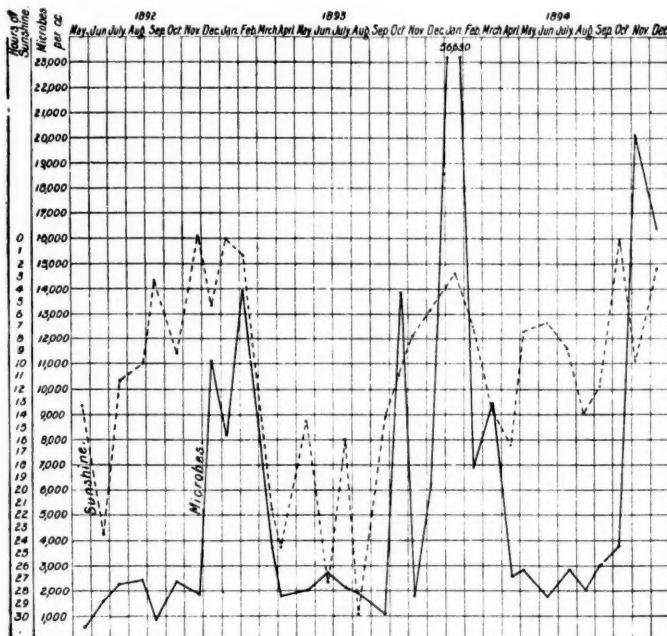


No. 7.

(2) the number of hours of sunshine on the day and up to the hour when each sample was drawn and on the two preceding days, and (3) the flow of the Thames over Teddington Weir on the same day expressed in millions of gallons per twenty-four hours. Although the graphic representations were confined to the Thames, the conditions affecting bacterial life in this river are doubtless equally potent in other rivers and streams.

The samples for microbe cultivation were collected at

about nine inches below the surface of the water in partially exhausted and sealed tubes, the ends of which, when the tubes were lowered to the required depth, were broken off by an ingenious contrivance devised by my Assistant, Mr. Burgess. On being withdrawn from the river the tubes were immediately hermetically sealed and packed in ice for conveyance to my laboratory, where the cultivation was always commenced within four hours of the time of collection.



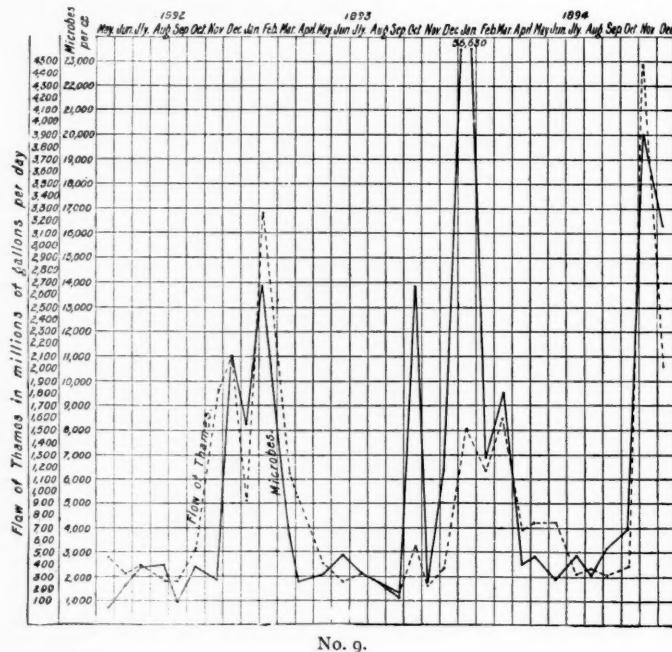
No. 8.

For the records of sunshine, I am indebted to the kindness of Mr. James B. Jordan of Staines; and for gaugings of the Thames at Teddington Weir to Mr. C. J. More, the engineer to the Thames Conservancy Board.

The graphic representation of these collateral observations affords definite evidence as to which of the three conditions—temperature, sunshine, and flow of the river—has the predominant influence upon bacterial life in the water. The first diagram (No. 7) compares the number of

microbes per cubic centimetre with the temperature at the time the sample was taken. The horizontal lines express the numbers of microbes and the temperature, while the vertical lines denote the months when the samples were taken. For obvious reasons the horizontal lines expressing the numbers of microbes and temperatures are numbered in opposite directions.

The diagram shows that although coincidences between a high number of microbes and a low temperature are not



No. 9.

wanting, some other condition entirely masks the effect, if any, of temperature.

The next diagram (No. 8) institutes the comparison between the number of microbes and the hours of sunshine to which the water has been exposed. The diagram is constructed on the same lines as the first.

It is here seen that, as in the case of temperature, there is some other condition which entirely overbears the influence of sunlight in the destruction of microbes in the

river water. This condition is the amount of rainfall higher up the river, or, in other words, the volume of water flowing along the river bed, as is seen from the comparison represented in the next diagram (No. 9).

This diagram shows very conclusively that the volume of water flowing in the Thames is the paramount influence determining the number of microbes. It compares the volume of water in the river gauged at Teddington Weir with the number of microbes found in the raw Thames water at Hampton on the same day. In this diagram, the numbers representing the flow of the river in millions of gallons per day and the number of microbes per cubic centimetre in the water both run from the bottom of the diagram upwards.

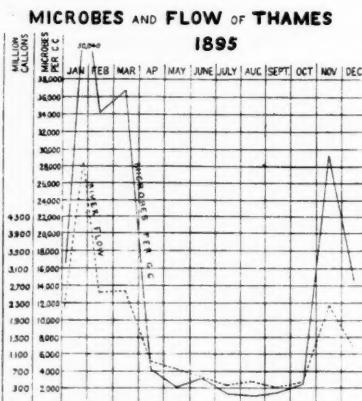
Comparing the curves in the diagram it is seen that, with very few exceptions, a remarkably close relation is maintained between them.

The only exception of any importance to the rule that the number of microbes varies directly with the flow of the river, occurring during the thirty-two months through which these observations were continued, happened in November, 1892, when the flow increased from 501 millions of gallons in October to 1845 millions in November, whilst the microbes actually diminished in number from 2216 to 1868 per cubic centimetre. Neither the sunshine nor the temperature records of these two months, however, afford any explanation of this anomalous result, for there was a good deal of sunshine in October before the collection of the sample and the temperature was higher, whilst in November no ray of sunshine reached the Thames during the three days preceding the taking of the sample and the temperature was nearly  $4^{\circ}$  C. lower than in the preceding month. I have ascertained, however, that the Thames basin had been twice very thoroughly washed out by heavy floods before the time when the November sample was taken, and this affords a satisfactory explanation of the anomalous result yielded by this sample.

These comparisons demonstrate that the number of microbes in Thames water depends directly upon the rate

of flow of the river, or, in other words, on the rainfall, and but slightly, if at all, upon either the presence or absence of sunshine or a high or low temperature; and they are confirmed by the continuation of these observations during the year 1895 exhibits in diagram No. 10.

With regard to the effect of sunshine upon bacterial life, the interesting observations of Dr. Marshall Ward leave no doubt that sunlight is a powerful germicide; still it is obvious that its potency in this respect must be greatly diminished, if not entirely annulled, when the solar rays have passed through a stratum of water of even com-



No. 10.

paratively small thickness before they reach the living organisms. By a series of ingeniously contrived experiments, Mr. Burgess has demonstrated the correctness of this view.

A sterile bottle about half filled with Thames water was violently agitated for five minutes to insure equal distribution of the organisms. Immediately afterwards a number of sterile glass tubes were partially filled with this water and sealed hermetically. Three of these tubes were immediately packed in ice, and the remainder were attached in duplicate at definite distances apart to a light wire frame which was then suspended vertically in the river. The

experiments were made near the Grand Junction Company's Intake at a place favourable for the sun's rays to fall on the river without any obstruction.

The river was at the time in a very clear condition and contained but little suspended matter; whilst the day was fine, although clouds obscured the sun occasionally. The tubes were exposed to light in the river for four and a half hours—from 10.30 A.M. to 3 P.M. on 15th May, 1895. At the end of this time the tubes were packed in ice for transport to my laboratory, where the cultivation was started immediately. The colonies were counted on the fourth day and yielded the results given in the table:—

	No. of Colonies per c.c.
Thames water packed in ice immediately after collection	2127
Thames water after exposure to sunlight for 4½ hours at surface of river	1140
Thames water after exposure to sunlight for 4½ hours at 6 in. below surface of river	1940
Thames water after exposure to sunlight for 4½ hours at 1 ft. below surface of river	2150
Thames water after exposure to sunlight for 4½ hours at 2 ft. below surface of river	2430
Thames water after exposure to sunlight for 4½ hours at 3 ft. below surface of river	2440

These experiments show that, on 15th May the germicidal effect of sunlight on Thames microbes was nil at depths of one foot and upwards from the surface of the water. It cannot, therefore, excite surprise, that the effect of sunshine upon bacterial life in the great mass of Thames water should be nearly, if not quite, imperceptible. It is thus ascertained that sunlight can only kill the germs, or microbes, near the surface of the water, whilst those at any depth, for the most part, escape destruction.

On the other hand the enormous effect of floods in augmenting the number of microbes can hardly surprise us, for when a great body of water has flowed over the banks of the river, which are at other times dry and exposed, it carries along with it countless impurities—an effect common both to the main stream and its tributaries. The Thames

basin is as it were, on every such occasion, thoroughly washed out, and it is only to be expected that the number of microbes in the water should be enormously increased as is found to be the case.

Now with respect to

#### THE WATER SUPPLY OF THE FUTURE.

In view of the rapid increase of the population of London, fears have from time to time been entertained that the water supply from the Thames basin, that is to say from the rivers Thames and Lea, supplemented by water from springs and deep wells within the basin itself, would soon be insufficient in quantity; whilst the quality of the water taken from the river has, up to a comparatively recent date, been considered unsatisfactory. On these grounds various schemes have, from time to time, been brought forward for the supply of the Metropolis from other river basins—from the Wye, the Severn, the river basins of North Wales, and of the Lake Districts of Cumberland and Westmoreland.

It is worthy of note, however, that all the Royal Commissions have arrived *unanimously* at the conclusion that the *quantity* of water obtainable from the Thames basin is so ample as to render the necessity of going elsewhere a very remote contingency.

I shall now endeavour to put, very shortly before you a few facts which, in my opinion, prove that, both as regards quantity and quality, the Thames basin will for a very long time to come afford an abundant supply for the Metropolis. There is indeed no river basin in Great Britain which affords such an abundant supply of excellent water as that available in the Thames basin.

Besides that which flows directly into the rivers, this water is contained in the Chalk, Oolite, and Lower Greensand, which are the best water bearing strata in the kingdom. From these rocks it issues in copious springs of unsurpassed organic purity. I have personally inspected every spring of importance in the Thames basin and have

analysed samples of the water. The results, in a very condensed form, are recorded in the annexed Table. Twenty-

SPRING AND DEEP-WELL WATERS IN THE THAMES  
BASIN.

Results of Analysis in Parts per 100,000.	Oolite. Average of 21 Samples.	Lower Greensand. Average of 5 Samples.	Chalk.	
			Springs. Average of 8 Samples.	Wells. Average of 36 Samples.
Total Saline Matters -	27.34	18.25	30.14	37.45
Organic Carbon - -	.035	.032	.041	.052
Organic Nitrogen - -	.012	.006	.010	.019
Hardness before boiling	22.5	10.5	25.3	28.0
,, after     ,,	5.5	3.6	4.9	6.5

one samples of Oolitic spring water were analysed, and every one of these was of even greater organic purity than the water delivered by the Kent Company, which I have always regarded as the standard of organic purity to be aimed at in all other Water Works.

Five springs issuing from the Lower Greensand were examined; and again, every one of these was of even greater purity, organically, than the Kent Company's water; whilst they were, on the average, only one-third as hard. Forty-six samples of water from the Chalk were chemically examined, and these also contained but the merest traces of organic matter.

All these samples from the Chalk were derived from sources where the water-bearing stratum is free from a covering of London clay; but, as soon as the Chalk dips beneath the London Tertiary Sands and clay, the quality of the water undergoes a remarkable alteration. The total solids in solution are greatly increased in amount, whilst the hardness is much mitigated, owing to the replacement of bicarbonate of lime by bicarbonate of soda. These waters are also of high organic purity; but, as the quantity is very limited, it is useless to dwell upon them. They

supply the Trafalgar Square fountains and the London breweries, and we can well afford to leave them to be converted into beer. For dietetic purposes there is no better water in the kingdom than the underground water of the Thames basin. For *sentimental* reasons I should like to see it conveyed to the works of the various companies in special conduits; but we have seen that, on *hygienic* grounds, it may safely be allowed to flow down the bed of the Thames if it be afterwards efficiently filtered.

So much for *quality*, now as to *quantity*; the basins of the Thames and Lea include an area of upwards of 5000 square miles. Of this rather more than one half (including the Oolitic, Cretaceous, and portions of the Tertiary Formations) is covered by a porous soil upon a permeable water bearing stratum. The remainder is occupied by the Oxford, Kimmeridge, Gault, and London Clays; being thus covered by a clay soil upon a stiff and impervious subsoil.

The annual rainfall of the district is estimated at an average of twenty-eight inches. The rivulets and streams of the Thames basin are formed and pursue their course on clay land. There are no streams on the Chalk. That which falls upon this porous stratum and does not evaporate sinks, mostly where it alights, and heaps itself up in the water-bearing stratum below, until the latter can hold no more. The water then escapes as springs at the lowest available points.

Innumerable examples of these springs occur all round the edge of the Thames basin, and at various points within it. Thus from the Chalk they are ejected at the lip of the Gault; and in the Oolitic area by the Fuller's Earth below it, or by the Oxford Clay, geologically, above it.

According to the guagings of the engineer of the Thames Conservancy Board there passed over Teddington Weir, in 1892, 387,000 millions of gallons, equal to an average flow of 1060 millions of gallons daily. In the following year, 1893, their passed over Teddington Weir an aggregate of 324,227 millions of gallons, or a daily average of 888 millions, the average for the two years being

974 millions of gallons, and this number does not include the 120 millions daily abstracted by the five London Water Companies who draw their supplies from the Thames.

Thus, in round numbers, we may say that after the present wants of London have been supplied from this river, there is a daily average of nearly 1000 millions of gallons to spare. Surely it is not too violent an assumption to make that the enterprising engineers of this country can find the means of abstracting and storing for the necessary time one-fourth of this volume.

As regards the quality of this stored water, all my examinations, of the effect of storage upon the chemical and especially upon the bacterial quality, point to the conclusion that it would be excellent. Indeed the bacterial improvement of river water by storage for even a few days is beyond all expectation. Thus the storage of Thames water by the Chelsea Company for only thirteen days reduces the number of microbes to one-fifth the original amount, and the storage of the river Lea water for fifteen days, by the East London Company, reduces the number on the average from 9240 to 1860 per cubic centimetre or to one-fifth; and lastly, the water of the New River Cut, containing on the average 4270 microbes per cubic centimetre contains, after storage for less than five days, only 1810, the reduction here being not so great, partly on account of the shorter storage, but chiefly because the New River Cut above the point at which the samples were taken, is itself a storage reservoir containing many days' supply after filtration. Indeed quietness in a subsidence reservoir is, very curiously, far more fatal to bacterial life than the most violent agitation in contact with atmospheric air; for the microbes which are sent into the river above the falls of Niagara, by the City of Buffalo, seem to take little or no harm from that tremendous leap and turmoil of waters, whilst they subsequently, very soon, almost entirely disappear in Lake Ontario.

It is not, therefore, too much to expect that storage for, say a couple of months, would reduce the number of

microbes in the Thames flood water down to nearly the minimum ever found in that river in dry weather, whilst, by avoiding the first rush of each flood, a good chemical quality could also be secured.

There is, therefore, I think, a fair prospect that the quantity of water derivable from the Thames at Hampton could be increased from its present amount (120 millions of gallons per diem) to 370 millions.

Again, in the river Lea, although here the necessary data for exact calculations are wanting, it may be assumed that the present supply of 54 millions of gallons could be increased by the storage of flood water to 100 millions per day. To these volumes must be added the amount of deep-well water which is attainable from those parts of the Thames basin which lie *below* Teddington Lock, and in the Lea basin *below* Lea Bridge, and which was estimated by the last Royal Commission at rather more than  $67\frac{1}{2}$  millions of gallons.

Thus we get the grand total of  $537\frac{1}{2}$  millions of gallons of excellent water obtainable within the Thames basin, the quality of which can be gradually improved, if it be considered necessary, by pumping from the water bearing strata above Teddington and Lea Bridge respectively, instead of taking the total supply from the open rivers above these points. Such a volume of water would scarcely be required for the supply of the whole water area of London at the end of fifty years from the present time, even supposing the population to go on increasing at the same rate as it did in the decade 1881-91, which is an assumption scarcely likely to be verified.

In conclusion, I have shown that the Thames basin can furnish an ample supply for fifty or more years to come, whilst the quality of the spring and deep-well waters and of the filtered river water would be unimpeachable. To secure these benefits for the future, storage must be gradually provided for 11,500 millions of gallons of flood water judiciously selected in the Thames Valley, and a proportionate volume in the basin of the Lea; whilst filtration must be carried to its utmost perfection by the use of finer sand than is at

present employed, and by the maintenance of a uniform rate during the twenty-four hours.

There is nothing heroic in laying pipes along the banks of the Thames, or even making reservoirs in the Thames basin. They do not appeal to the imagination like that colossal work, the bringing of water to Birmingham from the mountains of Wales, and there is little in such a scheme to recommend it to the minds of the enterprising engineers of to-day. Nevertheless, by means of storage, by utilising springs, by sinking deep wells, and by such comparatively simple means, we have, in my opinion, every reason to congratulate ourselves that for half a century at least we have *at our doors*, so to speak, an ample supply of water which for palatability, wholesomeness, and general excellence will not be surpassed by any supply in the world.

E. FRANKLAND.

## SOME RECENT MEMOIRS UPON OLIGOCHÆTA.

THE literature relating to this group of worms is summed up in my *Monograph of the Oligochæta* lately issued by the Clarendon Press; but so energetic are the unfortunately somewhat few workers in this particular subject that new facts have gone on accumulating with some rapidity since the publication of that work. It is my intention in the present article to offer the reader a *résumé* of this latest work with, naturally, some references to what has gone before.

It is agreed by all those who are acquainted with the terrestrial Oligochæta that their peculiar mode of life, their susceptibility to sea water, and the comparatively few chances of dispersal enjoyed by them, render their distribution highly important in estimating the relations between land masses now and in the past. This has an especial bearing upon the theory of the former northward extension of the Antarctic Continent, a matter upon which much has been written lately. To deal adequately with this large question would of course demand more space than can be allowed me. I shall content myself with referring solely to the evidence which is forthcoming from the study of earth-worms. Fortunately we are in possession of a considerable amount of information about the terrestrial Oligochæta of New Zealand and Patagonia; the former country indeed must be regarded as being better known perhaps than any quarter of the globe, excepting of course Europe. The extensive collections lately made by Dr. Michaelsen in South America have added largely to the number of species brought back by his predecessors. It results from an examination of the species found in the two countries that in both of them the prevailing types belong to the genera *Acanthodrilus* and *Microscolex*, particularly the former. Of the thirty-two indigenous species at present known from Patagonia and the more southern parts of the South Ameri-

can Continent, twenty are members of the genus *Acanthodrilus*, eleven are *Microscolex* and one is a *Perichaeta*. Besides these are a few obviously imported *Lumbricus* and *Allolobophora* from Europe or North America. I say obviously imported because these worms are only found in cultivated ground and near the coast; as civilisation is left behind these species decrease and are replaced by the truly indigenous species. Among the twenty species of *Acanthodrilus* are included two or three which occur in the Falkland Islands and in South Georgia. Turning to New Zealand we find that out of twenty indigenous species nine are *Acanthodrilus*, six belong to the closely allied genera *Octochaetus*, *Deinodrilus*, and *Plagiochæta*, three are *Microscolex*, while the two remaining are a *Perichaeta* and a *Megascolides*, two genera which are eminently characteristic of the adjoining continent of Australia. Between New Zealand and South America is a long stretch of ocean, sparsely scattered over which are islands of volcanic origin. From three of these islands earthworms have been collected. In Kerguelen and Marion Island is a species of *Acanthodrilus* peculiar to those islands, and I have lately received, and am describing in the forthcoming June number of the *Proceedings of the Zoological Society*, a second species of that genus from Macquarie Island. The significance of these facts will be more apparent when we consider how far the genera that have been referred to in the foregoing are distributed outside of this antarctic area. *Microscolex* is found in many parts of central and the warmer western regions of North America; it has been met with also in Europe, Algeria and Teneriffe. *Acanthodrilus* occurs in Australia where it is represented by three species, all of which however inhabit the eastern half of the island continent, that part in fact which is nearest to New Zealand; *Acanthodrilus* has one species in Natal, one in New Caledonia and two in North America.

We have evidently therefore a fauna of earthworms peculiar to the antarctic region, into which more northern forms have been able to make but slight inroads and from which but few stragglers have wandered.

As to other distributional facts and theories, it is probable that I have underestimated in my Monograph the distinctness of the Palæarctic and the Nearctic regions of Mr. Sclater. I was disposed to unite them into one Holarctic as Professor Newton has called it. Further investigations have tended to emphasise the justice of separating these two regions. This evidence has been mainly collected by the industry of Dr. Gustav Eisen, of San Francisco; but others whose names and memoirs will be found quoted in the list of literature at the end of this article have added details of importance. The North American continent is inhabited by a fair number of peculiar genera, of which *Diplocardia*, originally described some years since by Garman, has four species (partly referred to the undoubtedly synonymous genus *Geodrilus*); there are also peculiar to this region *Phoenicodrilus*, nearly related to the central and South America *Ocnerodrilus*, and *Sparganophilus*; of this latter genus the original species was found by Benham in the Thames; but as there are half a dozen American species it seems likely that its occurrence in England is a case of importation. *Bimastos* is a genus perhaps justly separable from *Allolobophora*, from which it chiefly differs in the large size (for a Lumbricid) of the glandular sac in which the efferent male ducts terminate. Besides these peculiar genera are a few species of the Central and South American genera *Ocnerodrilus* and *Kerria*, and of the almost world-wide *Benhamia*. *Aleodrilus* is an Acanthodrilid that Eisen is disposed to separate from *Diplocardia*; two species of *Acanthodrilus* complete the list of non-European inhabitants of the North American Continent. But in addition to these are a number of *Allolobophora* and *Lumbricus*—the characteristic forms of the Palæarctic region—two or three of which are, however, so far as our present knowledge goes peculiar to North America. These facts perhaps justify the retention of the Nearctic region, and they are perhaps also significant in that the peculiar forms are western in range—a possible indication of their approaching extirpation by European species introduced by commerce.

The original indigenous forms, South American in character, may be regarded as having been gradually driven to the west by the encroachment of artificially introduced species. In other respects the geographical regions indicated by the distribution of earthworms agree fairly well with the generally received scheme of Mr. Sclater. The Ethiopian region is peculiarly distinct; the Neotropical is also nearly if not quite as plainly marked; but the Oriental fades into the Australian, and it is indeed not easy to separate them at all.

The only other matter affecting the distribution of earthworms with which I shall deal here is the question of oceanic islands. Our information upon the subject is not however by any means extensive; the largest collection made is due to the energy of Mr. Perkins, and has been described by me in a paper communicated to the Zoological Society. These worms were gathered in the Sandwich Islands, and belong to a number of species of which only two (and a doubtful third) have not been found elsewhere; these two belong to the genus *Perichaeta*, a genus prevalent in tropical regions, especially of the old world. That the bulk of the species known from these and other oceanic islands are forms which have been in all probability introduced by accidental transference by man is rather what might be expected from the limited powers of independent travel possessed by these animals. There is at present no certain evidence that there are any truly indigenous earthworms in oceanic islands, with the exception of Kerguelen—a fact which as I have already hinted may be due to other causes.

To Linnæus only a single species of earthworm was known, his *Lumbricus terrestris*, now believed to have been a compound of more than one species. Grube in his *Familie der Anneliden*, published in 1851, reckoned up only forty-two earthworms, and of these one or two are now known not to be earthworms at all, and of the remainder many are unrecognisable or synonyms. Since that period the increase of new forms has gone on—of late with extreme rapidity; at the present moment we are acquainted with rather over 500 distinct and well char-

acterised species. And this estimate does not take into consideration subspecies or well marked varieties, and pays no attention to "species incertæ". Of aquatic Oligochæta 150 is about the number of known species; but this group is decidedly less known than the former. As with other groups of animals this great increase in the number of known species has added to our knowledge of anatomical fact, but rendered harder the formation of classificatory schemes. No indistinctness, however, has arisen to blur the perfectly sharp outlines of the group Oligochæta, no "intermediate" forms have been discovered whose relegation to the group is a matter of uncertainty or convenience. At the same time a few approximations in structure to the leeches on the one hand, and to the Polychæta on the other have been discovered; but these are in no case of first-rate importance. Perhaps the most remarkable is the description of the gills of the African genus *Alma*. This worm was originally described under that name by Grube in 1855. Thirty-four years later Levinsen, apparently in ignorance of Grube's paper, named a fragment of what was obviously the same worm *Digitibranchus*, and described in the same paper *Siphonogaster*, an Annelid characterised by a pair of long processes an inch or so in length, and of a spatula-like form arising from the eighteenth segment. These have been subsequently shown to be processes containing the outer section of the sperm duct which opens near to the extremity. Michaelsen showed that all these three worms are identical, and has thus been able to put beyond question the existence of a true earthworm<sup>1</sup> with branched retractile gills on the posterior segments of the body. It was not by any means clear from the earlier descriptions that the gilled worm was not a Polychæt. Among the lower aquatic Oligochætes there are at least three gilled forms, apart from *Dero* which has a circlet of ciliated processes, with vascular twigs lying round the anus. These forms are *Chætobranchus* of Bourne, and *Branchiura* and *Hesperodrilus branchiatus* of myself. In

<sup>1</sup> Structurally; in habit it is aquatic.

the two latter (which are allied to *Tubifex*) are contractile branchiæ, not branched however, on some of the posterior segments of the body. More numerous are indications of affinity with the leeches. I may, in the first place, refer to that group of parasitic Oligochæta, once placed among the leeches but now usually allowed to be true Oligochæta, for which Vejdovsky has proposed the name of Discodrilidae on account of their posterior sucker. An American genus *Bdellodrilus* has lately been studied with care by Moore whose results entirely confirm the placing of the worms among the Oligochæta and their removal from the leeches. Their chief points of likeness to the Hirudinea are (1) absence of setæ; (2) existence of jaws; (3) presence of a sucker; (4) median unpaired character of reproductive pores.

The first and last of these characters are, however, found in a few undoubted Oligochæta, for instance, *Anachæta*, as its name denotes, has no setæ, and besides Mr. Moore describes large gland cells in *Bdellodrilus* which may represent setigerous cells of Oligochæta. As to the median generative pores they are very frequent among Oligochæta. The reproductive organs themselves are decidedly upon the Oligochætous pattern. The gonads are entirely free from their ducts, and there is a single spermatheca, a structure entirely wanting among the true leeches. The male ducts are two pairs, opening freely by ciliated mouths into the coelom and uniting into a common terminal atrium. Their arrangement recalls that of the Lumbriculidæ. The ovaries are proliferations of the coelomic walls and their contents escape to the exterior by a slit in the body walls lined by epithelium, a kind of rudimentary oviduct paralleled in the Enchytræidæ, and in the Eudrilid *Nemertodrilus*. There is nothing leech-like about the reproductive organs, excepting the terminal penis—a structure, however, which is also found in many Eudrilids and in some other Oligochæta. The conclusions of the author that the Discodrilidae are Oligochæta slightly modified for a parasitic life is quite borne out by their structure. We may admit at the same time that this modification is in the direction of the leeches.

In addition to questions of relationship to other neighbouring groups, recent investigation has brought to light facts of interest in the anatomy of the Oligochaëta which bear upon the mutual affinities of the families and genera into which the order is divided. In this direction the main discoveries of importance relate to the excretory system. In all the simple aquatic genera each segment of the body contains a single pair of nephridia; as a rule these organs are wanting in the anterior segments, and Professor Bourne was unable to find any nephridia at all in *Uncinaria littoralis*. The absence of nephridia in the anterior segments of the body, however, also characterises certain earthworms. It was originally described by Perrier in *Pentodrilus*, and all the species of this genus (6) are in the same condition. More recently Benham and Eisen have shown that the same state of affairs characterises the aquatic Geoscolecid *Sparganophilus*. A distinction therefore between the Limicolæ and Terricolæ of Claparéde quite breaks down. That these genera have no gizzard or calciferous glands (or at most the rudiments of a gizzard) is evidence of general degradation, which may have something to do with their aquatic or semiaquatic existence. It suggests too that the simplification in structure of the Limicolæ of Claparéde may be rather due to degeneration than to the retention of primitive characters.

Among the earthworms, however, the single pair of nephridia to each segment is far from being the rule. In a large number of genera the nephridia are multiple. Two pairs in each segment exist in *Brachydrilus*; three pairs in *Trinephrus*; and Eisen has lately shown that in certain North American Benhamias there may be three or four distinct and separate pairs each with its own internal funnel and external pore. The complexity of the excretory system culminates in *Perichaëta* where a single segment may be furnished with probably at least one hundred external nephridiopores. It is, however, a question whether in this latter case there is really an intercommunication between the several nephridia of each segment, and between those of adjacent segments as has been alleged by Spencer

and myself. The matter requires renewed investigation. In any case Bourne, Vejdovsky and I have shown that the "plectonephric" condition, as Benham has termed these diffuse nephridial tubes, is preceded by a series of paired nephridia one pair to each segment. This has been proved in *Perichaeta*, *Octochætus* and *Megascolides*. The nephridium elongates and becomes thrown into loops, each loop finally appears in *Megascolides* to break away and to form a distinct and separate nephridium. It is clear, therefore, that whether or not the connection is retained in *Octochætus* and *Perichaeta* there is originally a connection, so that that matter is of less importance than the alleged intercommunication from segment to segment. This multiple arrangement of the nephridia is only found in the families Acanthodrilidæ, Perichaetidæ and Cryptodrilidæ, and is the principal argument for uniting them into one superfamily, Megascolicides, as I have done in my Monograph. *Brachydrilus*, however, is a member of the family Geoscolicidæ, but it has only two pairs of nephridia to each segment; there is nothing like the complicated system of *Perichaeta*. This family Geoscolicidæ has been through the recent researches of Rosa and Michaelsen brought still nearer to the Lumbricidæ. It was always difficult to separate them, mainly on account of the aquatic *Criodrilus*, now it is practically impossible unless we accept Michaelsen's intermediate family Criodrilidæ. The ornament setæ which used to be a distinctive mark of the Geoscolicidae have been found by Michaelsen in *Allolobophora mæbii* and in *A. lönnerbergi*; many Geoscolicidæ, e.g., *Microcheta* are distinguished by the fact that instead of a single pair of spermathecae in each of those segments which contain them there are a considerable number of minute pouches; this distinction, however, falls to the ground since more than one *Allolobophora* is now known to possess the same character—which has moreover been met with in *Perichaeta*. It is in these two families that most instances are met with of total absence of spermathecae; *Kynotus*, a Madagascar genus, is anteclitellian like the Lumbricidæ, and in short it seems impossible to lay down any

set of characters which should absolutely separate the two families. Several members of the two families are aquatic; thus among the Geoscolicidae *Bilimba* (with which Michaelsen now suggests to unite Horst's *Annadrilus* and *Glyphidrilus*), *Criodrilus*, whose range the same author has lately extended to South America, *Alma* and *Sparganophilus*. Of Lumbricidae *Allurus* is the only form which is often aquatic. Michaelsen has dwelt upon the fact that all of these, with the exception of *Sparganophilus*, have the body generally or at least the posterior region markedly quadrangular in outlines with the setæ implanted at the four corners. This is an apparent consequence or at least concomitant of aquatic life which is more curious than explicable. So much then for recent modifications of the systematic arrangement of the group. I shall deal finally with various anatomical and histological discoveries which have a general interest unconnected with systematic relations. The most important work under this heading is undoubtedly the recent investigations into the structure of the remarkable family Eudrilidae, a well-defined family whose boundaries have not become in the least indistinct by the discovery of new forms. The family is remarkable on account of its distribution as well as on account of certain anatomical peculiarities. It is limited to tropical Africa—to the Ethiopian region of Sclater, with the sole exception of the type genus *Eudrilus*, whose ubiquitously, however (America, West Indies, India and the East generally, New Zealand, etc.), makes one suspect direct transference by man. This family is chiefly interesting on the anatomical side by reason of the illustration which it gives of two phenomena, *viz.*, substitution of organs and change in function of organs.

In all Oligochaeta the ovaries are paired (rarely unpaired) structures which arise from the peritoneal epithelium of the earthworms invariably the thirteenth segment. They are totally unconnected with the oviducts whose open mouths are placed exactly opposite to them. In the Eudrilidae these gonads are enclosed in sacs which communicate with a system of sacs the complexity of

which varies in different genera, and of which it would be impossible to give any detailed account without the assistance of figures. There is a separate *receptaculum ovorum* like that of the common earthworm, with which is connected the oviduct. This system of sacs, through which the ova can travel in so far as there are no physical hindrances, also contain sperm, and play the part of spermathecae or a spermatheca. They commonly open by a single ventral pore; sometimes the structures are paired as in the genus *Eudrilus* itself. Now these pouches generally contain sperm, and there is therefore the possibility of the ova being impregnated within them; Michaelsen has even suggested that some species are viviparous. In a few genera, for example in *Heliodrilus*, these pouches do not communicate with the exterior except through the oviducts. They appear to do so by a large ventral pore, but when careful sections are made it is found that this pore is the mouth of a closed sac, exactly like a spermatheca, which is enclosed within the large pouch. Thus the coelomic nature of this system of sacs is established on anatomical grounds, and developmentally they have been shown, at least in one genus, to be derivatives of the intersegmental septa just as are the sperm sacs of other earthworms; their cavities are therefore separated portions of the general coelom. But, as already mentioned, in most cases they do open on to the exterior directly by a conspicuous orifice, and contain sperm which probably finds its way into them by this orifice. The fact that in some cases these sacs contain structures which are precisely like the spermathecae of other earthworms, and that in other cases where they open directly on to the exterior the character of the lining epithelium changes near to the orifice, becoming distinctly columnar, suggests that we have to do here with the substitution of sacs derived from the septa for the true spermathecae which are gradually disappearing, only the extremity being left in the majority of cases. The second point with which I wish to deal concerns the calciferous glands. Most, but by no means all, earthworms possess one or more pairs of these organs, which are attached to and open into the oesophagus. What-

ever may be their functions they contain crystals of carbonate of lime, and have a rich vascular supply, the lining epithelium being much folded and therefore extensive. In some *Eudrilidae* these structures are absent or rather are so altered that they are nearly unrecognisable as calciferous glands. At the same time they have become more numerous. The structure is altered in that instead of an extensive lumen produced by the folding of an excretory epithelium there is a very short sac connected with the oesophagus, which is, however, enveloped by an extensive coating of cells which I regard as cœlomic cells, and among which meander abundant blood-vessels. These cœlomic cells, where they abut upon blood-vessels, very often lose their oval or rounded form and become columnar and at the same time more darkly staining. They surround the blood-vessel as if it were the lumen of a secreting gland, the cells themselves having acquired the appearance of a secreting epithelium. These phenomena suggest that we have to do here with a change of function on the part of the calciferous glands ; that their function of producing carbonate of lime, that their connection with alimentation has disappeared or is disappearing, and that a new function more intimately connected with the vascular system has supervened. There is a certain analogy here with the vertebrate liver which has certainly more functions than that of pouring bile into the intestine, though originally it may have been merely an annex of the alimentary canal.

In histology there is only one matter to which I shall direct the attention of the reader. It concerns the minute structure of muscular fibres in the *Oligochaeta*. The careful researches of Cervantaine have established the fact that the *Oligochaeta*, like the leeches, have muscular fibres which consist of an outer sheath often radiately striated, the muscular substance, and a soft central core. Hesse, however, while admitting this, goes a step further and endeavours to prove a resemblance to the muscular fibres of the *Nematoidea*. He figures in the *Enchytræidæ* and in the *Lumbricidæ* a gap in the sheath of the fibre through which the soft less-modified protoplasm of the interior com-

municates with a pear-shaped nucleated body outside. If these observations prove ultimately to be correct it is clear that there is a close resemblance in this particular between the Oligochæta and the Nematoidea.

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F. E. BEDDARD.

## NOTES ON ATOMIC WEIGHTS.

**I**N a former article<sup>1</sup> a sketch of the state of our knowledge as to the relative atomic weights of hydrogen and oxygen was given. It was there shown that although the great mass of the evidence was in favour of the atomic weight of oxygen being about 15.88 times that of hydrogen yet there was a certain amount of experimental work by well-known and tried observers which seemed irreconcilable with this result, the chief paper (1) being that of Professor Julius Thomsen of Copenhagen, and based on the proportion by weight in which ammonia and hydrochloric acid combine to form neutral ammonium chloride. In a short paper by the late Lothar Meyer (2) it was proved conclusively how little value could be attached to a determination of this nature however accurate and careful the manipulative work might be.

Any hopes which might have survived in the minds of the most ardent follower of Prout, that the atomic weight of oxygen is exactly sixteen times that of hydrogen, must now be dispelled by the recent publications of E. W. Morley (3) and of Thomsen (4) himself. The work of Morley is so conclusive, and has been carried out with such untiring patience and skill, that to any one who reads the clear account which he gives of his methods and of the various checks employed, it must be quite evident that that type of worker of whom we regard Stas as the chief is not yet extinct, in spite of the prevailing view that one must publish as many papers as possible in the least possible time before one can be said to engage in "original research". Morley's scheme for the complete determination of the relative atomic weights of oxygen and hydrogen is a most ambitious one, and, although his results are quite conclusive now, it is much to be regretted that bad health and other circumstances over which he had no control (such as a workman pushing a brick through a wall on to a

<sup>1</sup> August, 1894.

delicate piece of glass apparatus) have up to the present time prevented him from carrying out his original programme in its entirety.

The paper consists of four distinct parts—

- I. The determination of the weight of a litre of oxygen.
- II. The determination of the weight of a litre of hydrogen.
- III. The ratio by volume in which these two gases combine to form water.
- IV. The synthesis of water from known weights of hydrogen and oxygen, the weight of the water formed being also accurately determined.

It would be impossible to give any idea of the precautions taken to obtain results free from all objections in a sketch so short as this must be, for such details the original memoir must be consulted; only a summary of the results obtained can here be given.

Three methods were adopted to determine the weight of a litre of oxygen. In the first method the barometer and thermometer were used, and the gases weighed in balloons holding in three of the experiments about 9 litres, and in the other six about  $21\frac{1}{2}$  litres.

In the second method a globe of pure and dry hydrogen was used as the standard for temperature and pressure, the globe containing the oxygen having its pressure determined at the same temperature as that of the hydrogen by means of a very sensitive differential manometer.

In the third method the globes were filled with oxygen when they were immersed in melting ice and the pressure accurately determined at the moment of closing. This method had the disadvantage of wetting the surface of the globes, and probably thereby changing their weight (although this was duly investigated).

The values obtained by these three methods for the weight of 1 litre of oxygen under normal conditions of temperature and pressure at sea level in lat.  $45^{\circ}$  were

By use of thermometer and manometer - - - - -  $D = 1.42879 \pm .000034$ .

By compensation - - - - -  $D = 1.42887 \pm .000048$ .

By use of ice and barometer - - - - -  $D = 1.42917 \pm .000048$ .

From various considerations taking into account errors incidental to certain methods and liability to constant errors Morley gives the most probable value as  $1.42900 \pm 0.000034$ .

In the same way experiments were made with hydrogen and in five series but practically by three methods.

First method was practically the same as the first series of oxygen experiments.

Second method was like the third oxygen series.

Third method utilised the power of absorbing hydrogen possessed by palladium. The hydrogen was weighed in the palladium and expelled into globes, and its volume and pressure determined at the temperature of melting ice. Series III., IV. and V. were made by this method, but the apparatus employed varied somewhat in the various series.

The values which result from these experiments are

Series I.  $D_h = 0.89938$  gram.

Series II.  $D_h = 0.89970$  gram.

Series III.  $D_h = 0.89886 \pm 0.000049$  gram.

Series IV.  $D_h = 0.89880 \pm 0.000088$  gram.

Series V.  $D_h = 0.89866 \pm 0.000034$  gram.

The higher results of Series I. and II. are possibly due to some constant error, probably traces of mercury vapour. The most probable value is

$$D_h = 0.89873 \pm 0.0000027 \text{ gram.}$$

Part III. of the paper begins with a sketch of the methods it was proposed to employ to determine the volumetric composition of water. Of the three methods proposed Morley unfortunately has only been able to carry out the one which is the least satisfactory, *viz.*, the determination of the density of electrolytic gas and of the excess of hydrogen over and above what the oxygen can unite with. Leduc made a similar density determination, but apparently assumed that the hydrogen and oxygen were in the exact proportions in which they would recombine to form water. Morley found that he always had an excess of hydrogen when he kept his voltameter in ice and water, but that when the temperature was allowed to rise to about  $20^{\circ} \text{ C.}$  then oxygen was in slight excess, so that no doubt at a

certain temperature the gases do come off in atomic proportions. In each experiment the weight of the gases given off was about 23 grams.

The weight of a litre of the gas thus given off from solution of soda made from clean sodium was—

$$0.535510 \pm 0.000010,$$

and corresponds to a mixture of one volume of oxygen with 2.00357 volumes of hydrogen, but the excess of hydrogen was found to be 0.00088 giving therefore the ratio in which the gases combine as 1 : 2.00269.

Part IV. gives an account of experiments in which hydrogen was weighed in palladium foil, oxygen was weighed in a globe, these were then made to combine, and the water produced was weighed also.

From these experiments we get the following values for the atomic weight of oxygen :—

(1) From the ratio of hydrogen and oxygen, - - -	15.8792
(2) From the ratio of hydrogen and water, - - -	15.8785
or as a mean, - - - - -	15.879

From Parts I., II., III. of the memoir we get

$$\frac{1.42900}{0.89873} \times \frac{2}{2.00269} = 15.879$$

How excellent Morley's work is can perhaps best be seen by comparing his results with the means of those of previous experimenters,

	Rayleigh's summary.	Morley.
Density of oxygen at Paris, - - -	1.42961	1.42945
Density of hydrogen at Paris, - - -	0.8991	0.89901
Ratio of densities mean of all previous determinations, - - -	15.9005	
Ratio of densities, Morley's, - - - - -		15.9002
Ratio of combining volumes, Morley, -	2.00269	
" " Scott, -	2.00285	
" " Leduc, -	2.0037 (corrected = 2.0024)	

Although the results obtained by Thomsen agree wonderfully well with those of Morley it is not because his apparatus and his methods of working are so carefully elaborated. On the contrary what strikes one most forcibly is the extreme simplicity of the apparatus and mode of

working it as well as the neglect of certain precautions which could well have been taken, and ought to have been taken in an attempt to settle such an important constant as the present ; such precautions as to weighing with counterpoises of equal volume, for example, seem to have been neglected.

The method was to determine, firstly, the weight of hydrogen given off from unit weight of aluminium when dissolved in strong potash solution ; secondly, by supplying oxygen to a small combustion chamber so as to burn the hydrogen evolved from a known weight of aluminium, and collect all the water formed in the apparatus, one gets thus the gain of the equivalent amount of oxygen to the hydrogen and to the aluminium. The only corrections not of the simplest order were due to the oxygen and hydrogen remaining in the apparatus or which had to be evolved after the combustion had ceased. It was not found possible to burn all the hydrogen evolved completely as the current became so very slow when a very little aluminium remained undissolved. The aluminium did not require to be perfectly pure as long as it gave off no other gas than hydrogen. It was found that 162.3705 grams of aluminium gave off 18.1778 grams of hydrogen giving the ratio

$$\frac{\text{Hydrogen}}{\text{Aluminium}} = 0.111902 \pm 0.000015$$

as the mean of twenty-one experiments.

The weight of oxygen required to combine with 86.9358 grams of aluminium (or rather with the hydrogen evolved by its solution in potash) was found to be 77.1876 grams from which we get the ratio

$$\frac{\text{Oxygen}}{\text{Aluminium}} = 0.88787 \pm 0.000018$$

from which two results we get

$$\frac{\text{O}}{\text{H}_2} = \frac{0.88787}{0.11190} = 7.9345$$

$$\text{or } \frac{\text{O}}{\text{H}} = 15.8690 \pm 0.0022$$

We seem to have every reason now to regard it as completely proved that the atomic weight of oxygen is 15.87 to

15.88 times that of hydrogen, the higher value being in all probability the more correct.

Having now satisfactory determinations of our fundamental ratio we still require other ratios to be able to determine conveniently the atomic weights of many elements. If an element forms many compounds with oxygen it is never safe to conclude without the most rigorous proof that we have a pure oxide absolutely free from the other oxides of the same element. Hence determinations of atomic weights made by the reduction of oxides to the element or of one oxide to a lower one or of the oxidation of an element to an oxide or of one oxide to a higher oxide must always be accepted with caution. The use of the haloid compounds (especially those of bromine), of many elements, is of the greatest value, and for this we require an exact knowledge of the ratio bromine: oxygen. For this we depend chiefly on the classical work of Stas. The publication of the complete works (5) of J. S. Stas under the able editorship of Professor W. Spring, of Liége, enables every one now to obtain in an elegant and convenient form these models and masterpieces of accurate research which were formerly so difficult to procure. How great the contrast between the work of Stas and too much of that turned out at the present day a glance at almost any page of his works will show. Every step was proved most conclusively, however simple and even axiomatic it may seem to us now, before he proceeded to more elaborate propositions and deductions. For instance, in his *Nouvelles Recherches* he begins by proving that ammonium chloride prepared from absolutely different sources and purified in different ways always contains exactly the same proportion of chlorine, and that the same weight of each sample precipitated exactly the same amount of silver from its solution in nitric acid. He obtained his ammonia from ordinary *sal ammoniac* after destroying any organic bases by a treatment with *aqua regia*, and from commercial ammonium sulphate by a similar purification, by heating it to a high temperature with strong sulphuric acid, and then oxidation with nitric acid, and from potassium nitrite by reduction in an

alkaline solution with purified metallic zinc. The ammonium chloride was sublimed now in a current of ammonia gas, now *in vacuo*, but the results obtained showed that for the complete precipitation of 100,000 parts of silver, 49,592 to 49,602 parts of ammonium chloride were required. In other words, the *extreme* difference in a large number of determinations carried out with very considerable modifications only amounted to one part in five thousand.

Having thus proved that a compound always contains the same proportion of its constituent elements it was essential for his purpose as well as for the complete establishment of the atomic theory to prove that the equivalent weight of an element was not affected in the slightest degree by the various elements with which it might combine. To take an example, silver combines with iodine to form the iodide, and with iodine and oxygen to form the iodate, and these compounds are represented by the formulæ  $\text{AgI}$  and  $\text{AgIO}_3$  respectively. It was just possible, one might even say probable, that the ratio of silver to iodine in the one compound might not be the same as that in the other, but that it would be modified by the large quantity of oxygen present in that other substance. If, however, the elements consist of small particles alike in all respects, such a variation would be impossible, and the relative masses of silver and iodine in the iodide and in the iodate must be absolutely the same. To prove this may seem very easy, but Stas found it by no means so, for whenever he prepared his silver iodate by precipitation from the nitrate, after the reduction with sulphurous acid there was always a small excess of silver over and above the iodine present. This he finally traced to a minute quantity of the nitrate being carried down mechanically by the iodate, but so firmly held that no amount of washing would remove it. By using other soluble salts of silver such as the sulphate and the dithionate, however, he was able to prepare silver iodate so pure that on reduction to silver iodide not the slightest trace of either silver or iodine remained in excess. In the case of that prepared from the nitrate the excess of silver only amounted to one part in

3,000,000. These simple experiments give us some idea as to how hard it is to obtain even very simple compounds in a state of absolute purity. Having thus laid the foundations for his further work, and shown that the combining proportions of elements are mathematically exact, Stas considered no labour too great if thereby he could obtain more accurate values for these proportions. Any work done since his determinations has only tended to uphold his values and to increase our admiration for his work.

The great value of very accurate experimental work has been most strikingly exemplified by Lord Rayleigh's determinations of the density of nitrogen (6). He found that the nitrogen which he could obtain from air alone by removing the oxygen was *very little* denser, but was *always* denser than that prepared from the air with the aid of ammonia by Harcourt's method, and that the nitrogen prepared from ammonia or from any compound had always the same density, and that this was still lighter than that partly from air and partly from ammonia. From this he concluded that besides nitrogen the atmosphere must contain another constituent still denser, which like nitrogen resisted the action of iron and copper as well as their oxides, even when very strongly heated. By combining the nitrogen with oxygen after the method of Cavendish, or by causing the nitrogen to unite with metallic magnesium, a new gas to which the name of argon has been given was finally separated by Rayleigh and Ramsay after much laborious work. The detection in the atmosphere of a constituent hitherto unsuspected as well as its isolation are apparently only the first fruits of a number of more or less startling discoveries flowing directly from Lord Rayleigh's very accurate work. The molecular weights of argon (7) and helium (8) are respectively 40 and 4, and if their molecules are monatomic this would give us the same numbers for their atomic weights, but if the molecules are diatomic, as is probable, these numbers would be halved for the atomic weights. It is far from certain that either what we call argon or what we call helium is not a mixture of several similar substances.

Several atomic weights have been redetermined with great care, and of these determinations perhaps those of T. W. Richards of barium and of strontium are the most accurate and most interesting. By an exhaustive research on barium bromide he deduces the value  $Ba = 137.434$  ( $O = 16$ ) (9). From a similar study of barium chloride the value  $Ba = 137.440$  is deduced (10).

This value is notably higher than that usually accepted and is no doubt due to the careful elimination of small quantities of strontium and calcium which have contaminated the preparations of earlier experimenters. From a study of strontium bromide Richards found  $Sr = 87.659$  ( $O = 16$ ) (11).

Still more recently the atomic weight of zinc has been determined by Richards and Rogers again by means of the bromide and precipitation with silver, and as a mean they find the value ( $Zn = 65.404$ ) ( $O = 16$ ) (12).

In all the above determinations Richards estimated the percentage of silver in his haloid silver salt and showed it to be identical with that found by Stas, thus placing his work on the same footing and guaranteeing in this way its very high accuracy.

In 1888 two other American experimenters, Burton and Morse (13), published the results of their work on the same atomic weight which they arrived at by means of the conversion of the metal into the oxide by treatment with nitric acid and ignition of the nitrate. Although their work agrees throughout very well the value found is lower than that of Richards, due no doubt to the retention by the oxide of oxides of nitrogen as Marignac pointed out. In defending their work against this objection they expose their want of knowledge of the commonest reactions in such a way as to make one distrust all their work. The perusal of their paper provides much food for reflection of a serious nature although it does give a certain amount of instruction as well as amusement. They carry out their weighings to '00001 of a gram and pretend to detect differences of this minute amount in porcelain crucibles which have been heated up to the melting point of steel. In their account

of the purification of metallic zinc by distillation *in vacuo* it is rather odd to find it stated that indiarubber tubing with glycerine joints could not be used because *the vapours of zinc and of glycerine interact*. What pressure of the vapour of each is likely to exist at the highest temperature to which the joints would ever be subjected? The presence of gold in the nitric acid distilled from a platinum still, and coming from the gold solder used in it sounds also rather peculiar. One knows that very finely divided gold will dissolve in fuming nitric acid if kept cold, but one could hardly have thought of finding it as an impurity in nitric acid prepared by distillation. But the gem of all the statements comes at the end of the paper when these two rising experimentalists proceed to criticise Marignac's work (14), and finally to teach him and us how we ought to test for oxides of nitrogen by means of starch and potassium iodide. After proving to their own satisfaction by a process which cannot reveal the presence of any of these oxides that they are therefore obviously absent, they conclude that Marignac was ignorant of the necessary precautions which must be taken to exclude oxygen, especially that of keeping the solution practically boiling so that the steam may keep out the air. It is usually accepted as a well-established fact that the delicacy of this reaction decreases rapidly with rise in temperature, and that the colour goes completely before the boiling point is reached, even in the presence of relatively large quantities of free iodine.

Amongst other noteworthy determinations of atomic weights made recently are those of Winkler, who finds the values  $\text{Ni} = 58.91$  and  $\text{Co} = 59.67$  by means of the reaction between the chlorides and silver (15); and still more recently  $\text{Ni} = 58.71$  and  $\text{Co} = 59.37$  (16) by determining the amount of iodine required to unite with the pure metal. Winkler uses the value  $\text{Ag} = 107.66$ , if we use  $\text{O} = 16$  or  $\text{Ag} = 107.93$  these last values become

$$\begin{aligned}\text{Ni} &= 58.863 \\ \text{Co} &= 59.517\end{aligned}$$

The determinations of the atomic weight of boron by

Ramsay and Acton (17), as well as by Rimbach (18), are very interesting as examples of various methods of attacking this problem, and which give fair results, but they can hardly be said to have given results possessing greater accuracy than those of Abrahall (19).

Of all the elements of which the atomic weights are still in doubt, and of which the determinations are very unsatisfactory, by far the most interesting is undoubtedly tellurium. According to the periodic classification of the elements it ought, as is well known, to have an atomic weight less than that of iodine, but all the most satisfactory determinations are irreconcilable with this, and make the atomic weight notably higher than that of iodine. The experiments made in recent years both by Brauner (20) and by Wills (21) agree in this, no matter what method is adopted as long as it is one which gives concordant results. The latest determinations, those of Staudenmeier (22) which start from telluric acid, give, according to him, the values 127.6, 127.1, and 127.3 for three series of experiments in which different ratios were determined. He takes as his standard O = 16 and H = 1.0032. Staudenmeier upholds that tellurium is an element in opposition to Brauner who at one time maintained that it was a mixture of true tellurium with a higher homologue, but now concludes that this is very improbable, and since the discovery of argon suggests that the assumed impurity may be a homologue of argon. Speculations of this nature are strongly to be discouraged and condemned, especially when their basis is nothing more than the assumed abnormality in the periodic arrangement of the elements coupled with a very decided want of agreement in the results of an experimenter's own work obtained by different methods. They may afford an easier way out of a difficulty than by working steadily at the causes of such discrepancies, but afford at best but a feeble and undignified cover for one's retreat.

*P.S.*—About the middle of last month, and after the above article was written, Thomsen (23) published the results of some new determinations of the densities of oxygen and hydrogen. The oxygen was prepared by

heating a mixture of potassium chlorate and ferric oxide, and the hydrogen from a solution of caustic potash by the action of metallic aluminium. The values found were :—

Weight of one litre of oxygen at  $0^{\circ}$  C. and 760 mm. pressure, at sea-level in Latitude  $45^{\circ}$  - - - - = 1.42906 grams.  
And of hydrogen similarly - - - - = 0.089947 gram.

From these he deduces the ratio of the volumes in which they must combine to form water to be 1 : 2.00237.

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ALEXANDER SCOTT.

## THE STELAR THEORY; A HISTORY AND A CRITICISM.

### PART II.

#### THE METAMORPHOSES OF THE STELE.

IT is clear that the theory of polystely forms an integral part of the general stelar doctrine, and we can hardly refuse to accept its main idea. But though each stele in the polystelic stems of, for instance, *Auricula Ursi* and many Polypodiaceæ is clearly the equivalent of the whole cylinder in the hypocotyl of the same plants, cases exist in which we seem forced to consider as steles, vascular strands which have none of the characters of the cylinder left about them.

Deriving our idea of the typical stele from the monostelic organ, we come to consider it as essentially cylindrical and radially symmetrical. It is true that diarch roots are bilateral in structure, and the primary root and hypocotyl of very many ferns being diarch the steles of a great number of their stems are likewise diarch and hence bilateral. And this bilaterality often extends to the *shape* of the stele which becomes oval or band-shaped instead of circular in transverse section, the two protoxylems being situated at the extremities of the figure. Another step is for the stele to become more or less semilunar in transverse section, so that it is no longer symmetrical about the plane passing through the protoxylems, but only about the bisecting plane perpendicular to this. And further the protoxylems may lose their symmetrical arrangement, or one only may be present, and this may be excentrically placed (*Angiopteris*). We clearly could not tell that such strands were steles if we had no knowledge of their connexions and disposition. At least as far as tissue arrangement goes they may often be said to have lost those characters which entitle them to the name. A similar difficulty meets us in the case of the vascular strands in many fern leaves. Undoubted steles found in

the petiole, after repeated branchings gradually lose the phloem from their upper sides, and thus come to possess the collateral structure of the bundle of a Phanerogamic leaf. On the other hand the curved bundle in the petiole of *Osmunda* is certainly a meristele, if we may judge from its connexion with the bulky central cylinder of the monostelic stem, yet it is surrounded by a complete mantle of phloem, and indeed conforms in structure to many true steles (*cf.* 18). We may probably draw the same conclusion as to the "petiolar steles" of Gleicheniaceæ (19).

Similar facts appear to obtain in the polystelic genera of Phanerogams, upon which we may expect much new light from as yet unpublished researches. One instance is, however, too instructive to be omitted. A number of distinct steles arranged in a circle enter the peduncle of *Auricula Delavayi* (8, p. 304), fuse laterally, and become indistinguishable from a monostele, the central extra-stelar tissue passing over into pith.<sup>1</sup> Van Tieghem warns us (10, p. 768) not to confound such a structure formed in an essentially polystelic stem with an essentially monostelic stem. But if this sort of thing may occur, what guarantee have we that an "essentially monostelic" stem is really essentially monostelic, or, for the matter of that, that an "essentially polystelic" stem is really essentially polystelic? If a stele can become a collateral bundle in the course of a shoot system, the same transformation may very well occur, or a collateral bundle may become a stele, in the course of descent; at least we are quite debarred from dogmatically drawing or denying homologies between the one and the other. Of course we can speculate, and in some cases claim a fair degree of probability for our speculations, especially when we have a minute knowledge of all the facts in the anatomy of a given group, but since it is impossible to draw a sharp line between a stele and a vascular strand that is not a stele we are clearly not on very firm ground. There is certainly nothing to surprise us in this;

<sup>1</sup> A similar state of things appears to obtain in some of the Palm roots investigated by Mr. Cormack.

the instructive fact is that "there's such divinity doth hedge" a stele—indeed any morphological conception, as in almost every fresh case to prevent for a time our realisation of the truism that "Nature knows no sharp boundaries". In the stellar doctrine, we have, no doubt, a classification that enables us to perceive a little more closely the directions along which the various types of vascular system in the higher plants have been evolved, and that after all is the most we can expect.

#### DEVELOPMENTAL EVIDENCE BEARING ON THE STATUS OF THE STELE.

We have now to consider the developmental basis of the stellar theory. Let us take the Phanerogams first. It is well, as Dr. Scott (20) has already pointed out in this journal, to draw a distinction between development from the embryo, and development of the various axes from their permanently embryonic growing points. It is clear, on reflection, that the former alone is comparable to ontogenetic development in animals, though it would be a mistake to suppose that the latter is not of importance to morphology. In the comparatively few types of monostelic plants with the anatomy of whose embryos we have a sufficient acquaintance, it appears that both in the plumule and radicle there is really a clear separation at the apex between central cylinder and cortex (plerome and periblem). But it is certainly open to doubt whether this distinction, as Hanstein thought, is really maintained at the growing points of the various axes throughout the life of the plant. Into the history of the differences of opinion on this point we need not enter. The inherent difficulties of arriving at valid conclusions from observations have been nearly as powerful as the subjective causes which have evidently influenced the views of the observers in creating the extraordinary discrepancies which exist between the various accounts.

The method employed by Ludwig Koch (21 and 22), who recognised that the state of things at the growing point was likely to differ at different epochs of growth, and

that hence conclusions drawn from observation of a few sections could not be final, marks a great advance on previous work. Koch claims to have proved (22), in *Syringa* and *Berberis*, that the single layer of cells immediately beneath the dermatogen, *i.e.*, the periblem of earlier observers, divides periclinally, during a period of leaf formation, across the actual apex of the shoot, thus giving rise to three or four superposed layers of cells. It is clear that, if this is the case, all but the uppermost of these layers must become part of the plerome when the apex passes back to the state of possessing a single layered periblem. But though our author has convinced himself that this actually happens, his figures are not decisive. Most of the periclinal divisions which he shows in the periblem of the Lilac (Taf. xvi.) are clearly in connexion with the formation of the leaf rudiments. In no case are such divisions shown across the actual apex. In fig. vi. periclinal walls are drawn in two periblem cells removed by one cell from the cell-group obviously concerned in the formation of a leaf rudiment, but these walls are also removed by one or two cells from the centre of the flat growing point, and considering how much this free surface is encroached upon by the developing leaves (*cf.* fig. vii.) it is not at all clear that the periclinal wall in question is not precociously formed in a cell which will later be involved in the base of the leaf. Yet this single periclinal wall is really the sole evidence obtainable from his figures of the truth of Koch's view. Nevertheless the thorough method of investigation inaugurated by Koch must sooner or later settle the point. For the present we must admit that though Hanstein's case is made out for a certain small number of plants, the great majority of cases which have been investigated must remain doubtful. Van Tieghem (10, p. 776) does not definitely commit himself, though he implies the suggestion that Hanstein's three initial layers are universal in Phanerogams, though often not distinguishable owing to "enchevêtrement" of the layers. But his pupil Douliot (23) concluded that there was a single apical cell in all Gymnosperms, and a plero-periblem in most

monocotyledons and some dicotyledons, while Koch takes the view that there is a generalised meristem without separate layers in Gymnosperms (21) and that only the dermatogen is separate in most Angiosperms (22). So that the "triple layer" theory of Hanstein and Van Tieghem is accepted by neither of these two most recent investigators as of general application, widely divergent as are their views *inter se*. Considering that the theory of the direction of ontogeny by the separation of different kinds of somatic idioplasm is now generally discredited, it is difficult to see what we gain by an adherence to the unproved hypothesis of the strict separation of the initial layers, even if it is still a possible hypothesis.

In the root apex on the contrary the plerome is in the great majority of cases sharply separated from the periblem, but even this rule is not universal. The sharp separation seems to be correlated both in root and stem with the formation of a slender compact cylinder.

In Vascular Cryptogams, which nearly all possess either a single apical cell or a single layer of initial cells giving rise to the whole of the tissue of the axis, there is of course no question of a separation, at the apex itself, of initial layers.

The separation of the young cylinder behind the actual growing point is quite a distinct question from its separation at the apex. It is during the development of the cylinder that we get, usually at least, a distinct limit between it and the cortex which is often lost in the adult stem, and this is a point of great importance.

Long before the stellar theory was originated, most of the great anatomists, who laid the foundations of our knowledge of the histology of vascular plants, were practically agreed on the generality of this early separation. This is clearly shown in the terminology employed in designating the various regions.

Thus Sanio (24), tracing from the apex the development of the various tissues, showed that in many cases the young pith first became separated from an outer zone, and that in the latter the "thickening ring" (really corresponding to

Flot's "vascular meristem," *i.e.*, the ring of tissue producing the bundle system *plus* the "external conjunctive": shortly became differentiated from the peripheral zone or young cortex. In other cases (*Euonymus* and *Berberis*), the "thickening ring" appeared or began to appear *before* the young pith became separated from the "outer zone". Hanstein (25), as a consequence of his separation of the primary meristem into Dermatogen, Periblem and Plerome, makes the outer limit of the young cylinder, *i.e.*, that between periblem and plerome, of primary rank. Russow's scheme (26), on the other hand, drawn from instances like those of Sanio's first group,<sup>1</sup> in which the young pith is the first tissue to become apparent, divides the young tissue produced by the general Protomeristem at the apex itself into *Endistem* (Sanio's young pith) and *Existem* (Sanio's "Aussenschicht"), the latter being separated into *Mesistem* (Sanio's "thickening ring") and *Peristem* or young cortex. Thus the limit between "Mesistem" and "Peristem" is reduced to secondary rank. But De Bary (14, pp. 395-6) again sums up clearly in favour of the individuality of the plerome.<sup>2</sup> As a matter of fact the young pith often does

<sup>1</sup> Russow placed Hanstein's best instances, for example, stem of *Hippuris*, and Roots, where there is a well-defined plerome at the apex itself, under the separate heading of "Axes with Combined Bundles".

<sup>2</sup> The development of the pericycle is of great importance in this connexion. Sanio (24) showed in several cases that what we now call the pericycle was developed from the outer edge of the "thickening ring". Schmitz (27) confirmed this view in *Berberis* and *Menispermum*. Van Tieghem, however (5), based his conception of the pericycle entirely on the ground of adult comparative anatomy. This is explicitly stated (p. 152) in a remark he made at the close of a "Note sur le pericycle," read by D'Arbaumont (28) to the Botanical Society of France. D'Arbaumont had endeavoured to show that the sclerised portions of the pericycle, capping the phloems of the stem bundles in dicotyledons, were developed in common with the bundles themselves from the desmogen strands, and were thus often separate from the interfascicular pericycle. His account of the development of the continuous zone of fibres in *Cucurbitaceæ* and in *Berberis* is different, and indicates differences in the origin of the pericycle in various plants. It is unfortunate that no figures are given. Morot replied (29) that even if the pericycle, or parts of it, were developed differently in different plants, that made no difference to the validity or applica-

become recognisable in comparatively bulky apices (owing to the early ceasing of longitudinal divisions, and the stretching of its cells), before the outer limit of the young cylinder is defined. On the other hand, in the slender stems of many water plants, Hanstein's scheme applies with diagrammatic precision, the outer limit of the cylinder being clearly marked at the apex, before there is any sign of a differentiation between pith and bundle ring. But these differences of precocity in the development of the various regions of the cylinder, depending, as they do, upon the subsequent duration and size relations of the regions are clearly of little importance to morphology. The important fact which remains is the clear separation, slightly sooner, or slightly later, of the young cylinder from the cortex, in at any rate the vast majority of cases.

The separation thus made in development is, as a rule, more or less clearly maintained in the adult stem, though sometimes it is lost altogether. There is the possibility of a complete loss of a visible boundary between cylinder and cortex by the occurrence of irregular cell divisions in the young pericycle and inner cortex, together with a "shifting" (*Verschiebung*) of the original walls separating the two; unfortunately we do not know if this takes place in some cases or not. But apart from such an occurrence the distinction between cylinder and cortex, once made, is always made, and the layer of cells which once abutted on the young cylinder is still the phloem, not merely "theoretically," but in substance and in fact, however impossible it may become to distinguish it from the surrounding tissue.

It is these facts which form the real developmental basis of the stellar theory.

The phenomena (supposing them to be established) of real importance in the opposite sense, would be the occurrence of stems in which the external limit of the cylinder is never clear, of stems, in a word, which never possess a

tion of the term. The further pursuit of the theoretical implications of this statement would lead us into very deep waters, but it is clear that an extended comparative investigation of the origin of the pericycle is needed.

cylinder as such. While we could not admit that the stelar doctrine applied to such stems, we should probably be forced to the conclusion if their vascular system conformed in all other respects to the monostelic type, that the plants in question were derived from truly monostelic ancestors, whose descendants had lost the limit between cortex and cylinder.

The Nymphaeaceæ, many of whose stems contain a large number of "scattered" bundles, seem to furnish us with examples of such plants. Caspary (27) states that the bundles are here developed in centripetal order: this would seem to indicate an analogy with those plants (Piperaceæ, Begoniaceæ, etc.), which possess a proper bundle ring and also younger bundles in the pith, rather than with the monocotyledonous type. In at least one member of the family, *Victoria regia*, which possesses a particularly large number of these "scattered" bundles, it appears that no well-defined cylinder is visible anywhere in the stem.<sup>1</sup> So here if anywhere we seem to have a real case of "astely". We cannot, however, say the same with certainty of any dicotyledonous stem with a single ring of bundles. Nägeli's observations (28) indeed led him to the conclusion that the "cambial" strands were, as a rule, developed in the midst of a homogeneous ground tissue, but his conclusions, as we have seen, have been negatived by most subsequent observers.

Turning to the vascular cryptogams we find that whether monostelic or polystelic, the stele or steles can be traced nearly up to the stem apex. The first formed periclinal walls do not indeed necessarily mark the limit of stelar tissue. They may cut off the pith, as in *Equisetum* or mark the middle of the cortex, as in many roots, or the outer limit of the ring of steles, as in many fern stems, or of the single cylinder, as in the stolon of *Nephrodium* (10, pp. 692 and 773-4). Clearly no special importance can be attached to these walls, and we certainly cannot use the fact that they mark off the pith in *Equisetum*,

<sup>1</sup> I owe this information to the kindness of a friend in telling me the results of some unpublished observations.

as Van Tieghem does, to support the view that the genus is really astelic. This argument depends on the assumption that these walls always separate stellar from extra-stellar tissue, which is not a fact, according to Van Tieghem himself (10, p. 774), and further, a similar line of reasoning would tend to show that the stems of a great many dicotyledons, namely, those in which the pith is the first tissue to be marked off, are also astelic.

#### SUMMARY OF RESULTS.

We have attempted in the foregoing pages to exhibit, as clearly as possible, the bearing of well ascertained facts of anatomy and development upon the stellar theory as developed by Van Tieghem and his pupils. We may appropriately conclude with an attempt to summarise the results to which we are thus led.

We recognise in the central cylinder of the axes of the great majority of the higher plants an anatomical region of the first rank to be co-ordinated with the other great anatomical regions, the cortex and the epidermis. The central cylinder consists of vascular tissue (xylem and phloem) and conjunctive tissue (typically parenchyma). In the bulky typical<sup>1</sup> cylinder the vascular tissue is separable into distinct strands corresponding with its centres (or rather lines) of development, and giving to the cylinder a radial symmetry; the conjunctive of such a cylinder is separable into distinct regions. Typically, also, the innermost layer of cortex, which abuts on the cylinder is distinguished by special characters.

Reduced central cylinders are found in various stem structures, especially the thin stems of water plants. The reduction acts first on the conjunctive, which may (though rarely) quite disappear. This leads to the coalescence of the strands of vascular tissue into a more or less solid cylinder. Such a reduced cylinder is always sharply marked off from the cortex.

On the other hand we have stems in which it is impossible to separate the conjunctive from the adjacent

<sup>1</sup> In Sach's sense of "most highly developed".

cortical tissue. When this is the case in the adult, it is still often possible to make the separation in the young stem.

Naming the central cylinder a *stele*, we call all stems with a single cylinder *monostelic*.

Stems in which we cannot make the separation in any part, and which are therefore not strictly monostelic, yet conform more or less to the monostelic structure in other respects, and are no doubt usually derived in descent from the monostelic type.

Most Ferns and Selaginellas, and two genera of Phanerogams, while showing a monostelic structure in their hypocotyls, possess in their later formed stems more than one cylinder, each comparable in structure to the single stele of the hypocotyl. Such stems are known as *polystelic*. The steles of a polystelic stem may, however, take on the most various forms, and lose all the characters of the original cylinder; several may even coalesce to form a structure indistinguishable from a single stele. As this, or indeed the converse case of a non-stelar vascular strand assuming the characters of a stele, may have happened in descent without leaving any traces of the transformation, we are not justified in asserting the homology of all steles or denying homology between steles and non-stelar vascular strands. Nevertheless the stele is undoubtedly a real and relatively stable type in the arrangement of vascular tissue, and hence the name represents a real morphological conception.

The vascular tissue of a leaf is arranged in one or more strands, each of which, bilaterally rather than radially symmetrical, is called a *schistosteles* or *meristele*, representing, as it does, a part only of the stem cylinder. The meristele of a petiole may, however, simulate a stele. In most polystelic stems one or more of the stem steles directly enters the petiole, and the branches maintain more or less of the stelar character till near their endings in the lamina, where they become indistinguishable from collateral bundles.

We are probably justified in supposing the monostelic type to be primitive in vascular plants, and we may assume the original stele to have been relatively simple. To the increase in bulk of the stem and correlated increasing de-

mands for the supply of vascular tissue to leaves, the plant either responded by increasing the bulk of the stele and multiplying the number of its vascular strands, or by substituting a number of simple steles for the original single one. This last occurrence happened once at least in the Pteridophyta (probably more often), and more than once among the Phanerogams.

The primordial stele is represented at the present day by the single sharply defined stele of the embryo, which is maintained in the root and hypocotyl, and which passes over in the stem to one of the modern types of structure, necessary to the various demands of the leafy shoot. The arrangements at the apex of the latter are naturally adapted to form the particular type of structure in question, and can in no case be considered as representing an ancestral form.

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A. G. TANSLEY.

## THE PRESENT POSITION OF THE CELL-THEORY.

### PART II.

SINCE I have shown that protoplasm in the simplest form in which it is known to us may not be regarded as having an organisation in the sense in which that term has any meaning, and since it is a waste of time to discuss the use of the term when it has no meaning, we may more profitably turn to the question whether protoplasm has a structure, and if so, what kind of structure? Is it essentially the same in all the kinds of protoplasm which have been studied, and is it of the same kind as the structure of tissues and organs of metazoa or is it of a different kind? For it must be insisted upon that one may deny to protoplasm an organisation, in the proper sense of the term, and yet one may consistently attribute to it a structure, even a very complex structure. But that structure need not be called an organisation, to do so is to confuse two clear issues. It is worth while to emphasise this point, for some people think it very inconsistent to affirm that protoplasm has a complex structure and at the same time to deny that it is organised.

I conceive that the view that protoplasm is composed of granules, which are either biophors or secondary aggregates of biophors, has been sufficiently refuted by Butschli's researches on hyaline protoplasm already referred to. The hyaline pseudopodia of Gromia show no trace of granules, not because the granules are too small to be seen, for the highest powers of the microscope reveal in the protoplasm, at the moment of its protrusion to form a pseudopodium, a structure which is not granular, namely, an alveolar structure, and if granules were present they must necessarily be sought for in the alveoli or in the alveolar walls. But they are to be found in neither, so it may be affirmed that in the simplest form of protoplasm there are no granules, a circumstance which deprives the theory of biophors of much

of its weight. Of course it may be objected that the alveolar walls and contents may be composed of biophors so small as to defy detection; such an objection must be defended on theoretical grounds, and I will deal with it presently; just now I will confine myself to the consideration of the visible structure of protoplasm.

After rejecting the granular theory we have a choice of several others; the fibrillar theory, the reticular theory, and the alveolar theory of Bütschli. It would take too long for me to examine these several theories in detail; it has already been done by Bütschli (*loc. cit.*, p. 177), and still more recently by Yves Delage,<sup>1</sup> if I were to undertake the task I should only give a *résumé* of their arguments. For my own part I am strongly inclined in favour of Bütschli's "Wabenlehre".

For some reason or other Bütschli's account of the structure of protoplasm has not, to use a common expression, "caught on". Possibly because it was published at a time when men's minds were occupied with the more alluring prospect offered by the granular theory of protoplasm, with all its delusive hopes of an explanation by means of biophors, and primary organisation of the phenomena of heredity, and of all the vital processes. Possibly also because Bütschli himself pushed the analogy between microscopic foams and protoplasmic structure too far. But if his theoretical considerations are put aside, there is a great deal to be said for his fundamental views. The alveolar structure which he describes may be demonstrated in many various forms of protoplasm. It is particularly obvious in *Pelomyxa*, in which form the larger vacuoles serve admirably as a contrast between the finer alveolar structure which he claims to be common to all protoplasm and the grosser vacuolar structure which is often mistaken for it. I have myself identified the alveolar structure in a considerable variety of protozoa, and in a number of tissue cells, and I have succeeded in making Bütschli's artificial amoebæ, and am

<sup>1</sup> Yves Delage, *La Structure du Protoplasma et les Théories sur l'Hérédité et les grands problèmes de la Biologie générale*. Paris: C. Reinévald et Cie, 1895.

convinced of the close analogy in structure between the artifact and the natural product. The resemblance between the two is exact, and it is astonishing. The optical characters of the artificial product are explained, on physical grounds, as the outcome of a certain structure, namely, an alveolar structure. The identical optical characters of protoplasm may surely be explained on the same grounds. It is not pushing analogy too far to say that identical optical characters are the result of identity of structure. The analogy is somewhat strained when it is sought to prove that the identity of the streaming movements in the artificial product with those in protoplasm are attributable to the same physical causes. The chemical constitution of the two bodies is so different that the phenomena observed might be regarded as secondary. Nor is the identity absolute, for Bütschli himself points out that the induced currents in the surrounding medium take place in the reverse sense in an amœba to what they do in the case of the microscopic foam. I cannot think that the criticism of O. Hertwig invalidates Bütschli's theory seriously. Hertwig says that lamellæ of oil consist of a fluid which is not miscible with water. If the comparison between the structure of an emulsion and the structure of protoplasm depends on something more than a superficial resemblance, then the lamellæ of plasma which are compared with the lamellæ of oil must consist of a solution of albumen or of a fluid albumen. But a solution of albumen is miscible with water, and therefore it would mix with the contents of the alveoli: emulsions of albumen must be formed with air, not with water. To this Bütschli answered that the framework of plasma consists of a fluid composed of a combination of an albumen and a fatty acid, which was therefore not miscible in water. Another obvious answer is that living plasma is not a simple albuminous solution, for if it were most protozoa could not exist, they would immediately dissolve in the water in which they live. Whether a fatty acid exists in combination with the plasma or not, there is something in the constitution of living plasma which differentiates it from albumen, for it does not

dissolve in water ; dead plasma on the other hand becomes albumen and dissolves speedily. What that something is I do not venture to suggest ; could we ascertain what it is, no doubt we should have discovered the solution to the riddle of life. Hertwig says that the structural elements of protoplasm, be they filaments, or reticular, or lamellae, or alveoli, or granules, or what else, have a fixed state of aggregation. Protoplasm is no mixture of two immiscible substances such as water and oil, but consists of a union of fixed organic material particles with abundant water. This is but a verbal statement of the facts and is no explanation, but he adopts later on (*loc. cit.*, p. 49) Nageli's micellar theory as an explanation. No doubt it is the best explanation possible, but it again does not give more than a verbal explanation of the remarkable and fundamental phenomenon that protoplasm, be its structure what it may, does not when alive dissolve in water, but when dead it becomes something else which readily dissolves, provided of course that it is not killed by means which coagulate the albumens into which it is converted at death.

I shall recur again to the micellar theory, for the present purpose it is sufficient to say that it is not inconsistent with Bütschli's "Wabenlehre,"<sup>1</sup> and might even be pressed into service to explain why the plasma does not mix with the watery alveolar contents without the necessity of calling fatty acids to aid.

Supported by these considerations, and by a considerable mass of objective evidence, I venture to think that Bütschli

<sup>1</sup> Bütschli criticises the micellar theory and the analogous theory of "inotagmas" put forth by Engelmann. He does not accept either, but does not give in their place any theory of the ultimate compositions of the substances which form the alveolar framework and contents, except that (p. 309) he says, "a series of reflections . . . led me to suppose . . . that the chemical basis of the framework substance must be formed by a body which has arisen from a combination of albuminoid and fatty acid molecules." Such a combination must mean the formation of a chemical unit of a higher order than the molecules which enter into its composition, and for my purposes such a chemical unit is a micella. In this limited sense the acceptance of a micellar structure is not incongruous with the "Wabenlehre".

has given a true account of the minute structure of protoplasm, so far as it can at present be determined by optical means. And I even venture to prophecy that when the history of the biological work of this half century comes to be written some half century hence, the theories of biophors and plasomes and the such like will have merely a historical interest, whilst the work of Bütschli will be regarded as the most sagacious and far-sighted contribution of our time to this momentous question. In saying this I do not wish to declare my adhesion to the more theoretical part of Bütschli's work, but only to his account of the microscopic structure of protoplasm.

Even if one were to accept his explanation of the streaming movements there would remain all the other phenomena of life to be accounted for, and they are inexplicable on the visible structure of protoplasm, even if it be an alveolar structure.

Underlying the visible structure then there must be an invisible structure, which is the cause of the phenomena. This admission once made, the claims of the rival theories of biophors, plasomes, plastidules and what not, again press themselves on our attention. Now it is to be remarked that the most cautious and thoughtful theorists do not claim that their hypothetical units are an explanation of life. Weismann categorically denies that his theory of the germ plasm is a theory of life, it is only a theory of heredity, but he goes so far as to suggest that a workable explanation of the more complicated vital phenomena may be the surest indication of the path which will lead to an explanation of the more simple (*loc. cit.*, p. 21).

Others, however, are not so cautious, and in any case there is this feature common to all, that they aver on the one hand that vital processes are so complicated that they cannot be explained by a physico-chemical theory of the constitution of protoplasm, and that therefore we must assume the existence of ultimate vital units or biophors: on the other hand, after endowing these biophors with all the attributes of life, they say that they have a comparatively simple molecular constitution upon which the phenomena

which they exhibit depend. In fact they describe essentially similar functions in biophors and in cells, but they allow a physico-chemical explanation in one case and disallow it in the other. This contradiction has been noticed by others, and it has never been satisfactorily explained away. Whitman draws attention to it, and observes that no one, as far as he knows, has looked upon the unit as anything more than the seat of the mystery. This is true, but it is no reason for putting the mystery in a small bag instead of a big one. He defends the theories of smaller units, however, by saying that they have extended our knowledge of organic mechanism (*loc. cit.*, prefatory note, p. vi.). This again I believe to be true, but not quite in the sense in which Whitman apparently means it to be. The theories of minute independent vital units have, I believe, led many on the wrong track as regards vital mechanism; the attacks on such theories are leading to a considerable extension of our knowledge in this direction. The ultimate vital units confessedly do not remove the mystery; ultimately the explanation of life must be a chemico-physical one; there is no alternative but a vitalistic theory, and this is not admissible in science. The strongest ground, *viz.*, the granular hypothesis, for assuming the presence of vital units is removed by the observed constitution of hyaline protoplasm, and finally none of the assumed aggregates of units which are admitted to be visible, are identified with various sorts of granules and considered to constitute units of a higher order, have ever been shown to be capable of leading an independent existence.

On the other hand there is a general consensus of opinion that protoplasm is not a simple organic compound. Its unit is not the molecule, but an aggregate of molecules forming a unit of a higher order to which the molecule stands in the same relation as the atom does to the molecule. It is also admitted that these molecular aggregates may exist in many different kinds in protoplasm. Such a conception is absolutely necessary for the explanation of the most simple properties of organic bodies, for example,

their optical properties and the imbibition of water. But it is a physico-chemical conception, and the molecular aggregate need not and should not be endowed with independent vital powers. Such a molecular aggregate is the micella. In accepting the micella one may attribute any amount of complexity to protoplasmic structure without for a moment admitting that it is a congeries of elementary organisms. Nor need we admit all the theories which Nageli has tried to establish as the necessary consequences of the assumption that there are such things as combinations of polyatomic molecules into groups of a higher order. As I have already said, it was pointed out by von Sachs that even in the region of pure chemistry it is necessary to assume that polyatomic molecules are grouped into closer molecular unions, thus giving rise to chemical properties which did not belong to the individual molecules. But in the region of pure chemistry such a grouping is not called an organisation, nor is there any reason why it should be called an organisation in the present case. Let us be perfectly definite and say that by a micella we mean a combination of polyatomic molecules into closer union to form a group; nothing more, except in so far as we may reason on chemico-physical grounds as to the behaviour of such groups and their relations *inter se*. For instance (I am quoting from O. Hertwig's summary of this part of the micellar theory): "The micellæ exert an attraction both on water and on one another, whereby the phenomena of swelling may be explained. In a dry organic body the micellæ lie close to one another, separated only by exiguous envelopes of water: these latter enlarge considerably during imbibition, since the attractive forces between the micellæ and water are at first greater than between the micellæ themselves. The micellæ are separated from one another by the imbibed water as it were by a wedge; but an organised body does not arrive at a condition of solution, since the attraction of the micellæ for water diminishes in the course of their separation from one another, at a greater rate than the attraction of the micellæ for one another, and therefore, when the watery envelopes have attained a certain size, a condition

of equilibrium, the limit of imbibition is reached." And also : "Since particles of water may be held fast on the surfaces of the micellæ by molecular attraction, so also other matters (lime and siliceous salts, colouring matters, gelatin compounds, etc.) may be deposited on them after they have been taken into the organic body in a state of solution". So far as my physical knowledge enables me to form a judgment, attributes such as these may justifiably be ascribed to micellæ on purely physical grounds and their importance can hardly be overestimated, since the last passage quoted affords a hint as to the nature of the essentially vital process of assimilation. It is not my business now to develop a complete theory ; I doubt indeed whether a complete theory is possible in the present state of our knowledge. I have done sufficient for present purposes if I have succeeded in indicating what ideas we may justifiably hold on the subject of protoplasmic structure, and I believe that I have given some good grounds for justification of the views that ; (1) the ultimate visible structure of protoplasm is an alveolar structure ; (2) that the invisible structure of protoplasm is a "micellar" structure in the sense defined above.

But before I proceed I must enter a caveat against being considered as an adherent of the micellar theory of Nageli. I cannot enter here into my reasons, but I may say that the further theories which Nageli assumes to be the necessary consequences of the existence of micellæ, do not appear to me to be necessary consequences at all ; indeed I part company with him at once when I express my conviction that the hypothesis of a micellar structure is compatible with the alveolar structure described by Bütschli.<sup>1</sup>

<sup>1</sup> Since the above argument was first written out the work of Yves Delage has come into my hands. It is most gratifying to find that the opinions of so distinguished an author accord so exactly with my own. The reader who finds my argument involved and laborious may turn with profit to Delage's book, in which he will find a lucidity of expression and a precision in argument which I can only envy without hoping to imitate. It is worth while quoting the following passages here : "On peut accorder

I may now anticipate the objection which is certain to be raised that the visible and invisible structure which I assign to protoplasm is utterly inadequate to explain the phenomena of life. It is inadequate and it is intended to be inadequate. Were I to pretend that it is adequate I should be running counter to all the lessons taught by our experience of living things. The structure which I have assigned to protoplasm applies particularly to that simplest known form of it which we rarely meet with, but which we do meet with in exceptional cases, for instance in the pseudopodia of *Gromia dujardini*. But separate a protoplasmic corpuscle formed by the thickenings of the thread-like pseudopodia of this species from the rest of the animal; the corpuscle separated is not any longer capable of an independent existence, it soon perishes, it has all the structure which I have described, but it is not capable of independent life. Clearly then life is not the outcome of this structure, though the structure may play its part, and no unimportant part in the life processes.

When I have been speaking of protoplasm I have obviously been confining my attention to that form of it which is now generally distinguished under the name of Cytoplasm. Cytoplasm taken by itself is not living matter in the sense that it is capable by itself of maintaining an independent existence. The experiments of Nussbaum,<sup>1</sup> of A. Gruber and Verworn, confirmed by other observers, have

à l'auteur (Nägeli) ses Micelles. Leur constitution, leurs propriétés n'ont rien que de très admissible. Bien que leur mode de génération ne soit guère probable, il n'y a aucune raison positive pour le repousser. Mais l'arrangement des micelles et la structure de l'idioplasma sont invraisemblables au plus haut point. Nous avons démontré, au cours de notre exposé, que cet arrangement n'est pas de tout, comme l'auteur l'avance, le résultat nécessaire du seul jeu des forces moléculaires initiales ce n'est qu'à grand renfort d'hypothèses étagées l'un sur les autres qu'il arrive à faire disposer les Micelles en Files, les Files en Faisceaux, les Faisceaux en Cordons et les Cordons en un Reseau répandu dans tout l'organisme."

<sup>1</sup> It was Nussbaum who first introduced the method of dividing infusoria by artificial means, and the credit of having devised this very useful class of experiment belongs to him. In my previous article I inadvertently assign it to Gruber.

shown that pieces of cytoplasm cut off from the remainder of a protozoon are incapable of maintaining life and soon perish. If, on the other hand, a fragment of cytoplasm similarly cut off contains nuclear matter, it is shown to contain the attributes necessary to life, for the fragment does not perish but reconstitutes itself and becomes an independent living being. The converse also holds good. A nucleus or a fragment of a nucleus isolated from a protozoon, is incapable of life and perishes. But a nucleus or a fragment of a nucleus in conjunction with a fragment of cytoplasm is capable of life and constitutes an independent living being. The reasonable inference is that cytoplasm plus nuclear matter is indispensable for the performance of vital functions.

Now cytoplasm plus nuclear matter constitutes a cell.

I have elsewhere discussed at some length the definition of a cell,<sup>1</sup> and I have defined it as a corpuscle of protoplasm which contains nuclein. In the present state of our knowledge this definition seems the only one possible. The cell then consists of two essential substances, cytoplasm and a substance which is different from cytoplasm, both structurally and in chemical constitution, namely, nuclein. In a great majority of cells other substances are present which are different from both of these. Such substances are the centrosomes, that modification of cytoplasm which is called archoplasm, amyllum and aleurone grains and so forth. As far as we know, however, these substances are not essential to life, but are secondary products characteristic of differentiated cells. Recent researches on the structure of Bacteria and Oscillaria justify the assertion that cells exist in which these substances are absent. We know next to nothing about the presence or absence of centrosomes and archoplasm in the Protozoa, and it may be that further investigation will lead us to the conviction that these two are as essential to the life of these forms as the presence of cytoplasm and nuclein. Maybe not; in any case it does

<sup>1</sup> *Quarterly Journal of Microscopical Science*, vol. xxxviii., p. 137, 1895.

not matter for present purposes. It is sufficient to know that two substances, cytoplasm and nuclein, must be brought together or life cannot exist, and that it does exist in organisms in which these substances, and these only, can be detected, *viz.*, in Bacteria. This statement may appear somewhat hazardous, seeing that the presence of a nucleus is denied in several living beings, in bacteria, for instance, and in yeast. A nucleus in the sense of a centralised body is certainly absent in these and in many other forms, but Bütschli has demonstrated the presence of nuclein in *Oscillaria* in *Bacterium lineola*. As for *Saccharomyces* it undoubtedly contains nuclein, for Raum has prepared it from yeast cells, and the most recent observer, Macallum,<sup>1</sup> is of the opinion that the nuclein is distributed through the cytoplasm but also aggregated in the so-called granules of Raum.

The statement therefore can scarcely be called hazardous, and it is really warranted by the facts at our disposal, for the more carefully that researches are made, and the more delicate the methods of investigations employed, the more is the presence of nuclein demonstrated where it was not previously supposed to exist.

Macallum's paper, by the way, is of great interest, for he shows that nuclein is essentially the iron-holding substance in cells. Knowing as we do the close connection there is between the presence of iron and the due performance of the vital processes, this observation opens up a fruitful source of inquiry as to the dependence of life on chemical processes.

Throughout this argument I have tried to stick to the rule of drawing legitimate inferences from observed facts without wandering into the obscure regions of hypothesis. If I have been successful and have fairly stated the facts, and have drawn legitimate inferences, the conclusion which I come to must be admitted to be of considerable weight.

<sup>1</sup> A. B. Macallum, "On the distribution of Assimilated Iron Compounds, other than Hæmoglobin and Hæmatins, in Animal and Vegetable Cells," *Quart. Jour. Mic. Sci.*, vol. xxxviii., pp. 175-274, 1895.

The conclusion is this: *that life is possible only when two (or more) substances of complex chemical constitution are brought together, and that when these two (or more) substances are brought together we have before us a cell.* The cell therefore is the vital unit κατ' ἔξοχήν. The component parts of the cell are not vital units, for by themselves they are incapable of life; they are the auxiliaries, the indispensable auxiliaries of life, but they are not themselves living.

This is not a theory of life, and it does not pretend to be one. It is the generalisation which the facts seem to warrant, and if it be true, as I believe it must be true, it is entirely inconsistent with the whole group of theories based upon hypothetical biophors, gemmules, plasomes, physiological units, plastidules *et hoc genus omne*. Those theories are false. And the cell theory is not inadequate, but it is the only theory which our knowledge of structure and of life processes permits us to adopt, at least if we confine ourselves to that part of it which is essential, namely, that there is one general principle for the formation all tissues, animal and vegetable, and that principle is the formation of cells.

Cells are the ultimate vital units, though they are not the ultimate structural units; *they* are the Lebensträger, or biophors, and there are no living individuals lower than cells.

As I have made an effort to stick to facts and have slighted hypotheses, I shall doubtless incur the profound contempt of those superior persons who find no mental repose in things which can be clearly apprehended, but must leave the material support of earth and seek for rest on the unsubstantial pillows of cloudland. They will have abundant scope for exercising their contempt, for my conclusion explains nothing, and gives no clue to the problems of heredity.

As I have said in the earlier part of this essay, I have no intention to discuss here the complicated problems which are involved in the question of heredity. I take my stand on the position from which I started, namely, that if minute

vital elements occur at all, those same elements which make life possible and control assimilation and growth must also be the agents in bringing about the phenomena of heredity. I have shown that minute vital elements smaller than cells cannot be believed to exist, and it is clear that the phenomena of heredity cannot be explained by things which have no existence. This is a sufficient answer to those who would say that the phenomena of heredity are such that we must make use of a hypothesis of minute vital elements, which are at once the bearers of the vital qualities and the bearers of the heritable qualities (the historic properties if the expression is preferred) of protoplasm. It is not true that a theory of heredity is impossible unless such elements are postulated. Delage has brought forward a theory of heredity which discards altogether the use of hypothetical biophors. I pass no criticism on his theory, favourable or unfavourable, but call attention to it merely for the purpose of showing that a theory without biophors is possible. It is no argument to say that the theories based on ultimate vital units have largely extended our knowledge of heredity. The Ptolemaic system of astronomy largely extended men's knowledge of the movements of the heavenly bodies, but it was not on that account a true theory.

Moreover, it will be hardly fair to twit me with the fact that I renounce, for the present, an attempt to explain the most complicated manifestations of life, for this is only an essay, and makes no pretence to be the development of a doctrine.

It is not my present intention to frame hypotheses, not because I undervalue the use of hypothesis, but because I regard the first necessary step to be the formation of ideas appropriate to the facts.

Dr. Whitman has recently written quite a nice little lecture on the subject of fact and theory, and has directed it against myself in particular, winding up with a trenchant paragraph to the effect that the claim to a monopoly of fact reflects an arrogance which seems to be epidemic. This homily is fortified by quotations from von Baer,

Goethe, Huxley and Whewell. Now I never claimed a monopoly of fact, but that facts should receive a due share of recognition. Mutual service, as Whitman says, is the principle which ties theory and fact together ; quite so, but when theory runs altogether away from fact, the mutual service is wanting. Fact is a slow servitor, and drags heavily on the impatient feet of theory. The quotations from Goethe and Huxley do not lend support to the practice of making hypotheses, rather the contrary. "Experience, Reflection, Inference" is an excellent motto, but inference does not mean making hypotheses, nor yet does the necessary process of generalisation and classification which Huxley recommends. The passage quoted from the last-named author condemns the mere cataloguing of facts under the name of Science, but it does not countenance the reckless use of theory. As for Whewell's aphorism, let me commend to Whitman a study of what that author says with regard to the failure of the Greek schools of philosophy. They did not fail, he says, because they neglected facts ; the Aristotelian school may be held to have surpassed the moderns in its appreciation of the value of facts. The Greeks certainly did not fail for want of boldness in theorising, nor for want of acuteness, of ingenuity and power of close and distinct reasoning. Nevertheless with all help from the twin-service of fact and theory their philosophy was a failure, and why ? Because, as Whewell points out, their ideas were not distinct and appropriate to the facts. May not the same thing be said of many of the theories of cell life and of heredity which have been so much in vogue in the last few years ? It was my object when I wrote on Epigenesis and Evolution to show that some ideas then current, were not appropriate to the facts ; it has been my object in the present essay to show that certain theories on cell life, beautifully constructed and ingeniously defended as they have been, are not appropriate to the facts. I am far from undervaluing the use of theory, and when I took occasion before, as I have done again now, to emphasise the importance of attention to fact, I was not quite so ignorant nor so arrogant as Whitman supposed. The motto of Goethe

might well have been reversed for the adornment of the title pages of some works of the last twenty years. "Theory, reflection, experience," the last named to be fitted in as best it might.

Since the above passages were first written the great work of Yves Delage has came into my hands. Mine is not the only voice crying out in the great wilderness of theories. This new voice, however, is far greater and more powerful than mine. The reader who may be unconvinced by my clumsy argumentation should turn to the pages of Delage. For clear and candid exposition, trenchant criticism, and rigorous exposure of defects of reasoning, they are unsurpassed. Now that this part of my work is ended I feel that it need never have been begun, for all that I have had to say has been said in greater detail and with much greater force by Delage.

## FERNS, APOSPOROUS AND APOGAMOUS.

THE normal life cycle of ferns, owing to the microscopic character of their reproductive apparatus, long baffled the comprehension of botanists. But some half a century ago, starting with the observations of Naegeli and Suminski and culminating in those of Hofmeister, the whole course of their ontogeny has been cleared up. The fern plant, as ordinarily so-called, produces on the back of its leaves or fronds, countless numbers of spores, which are formed within minute capsules or sporangia. When these spores germinate they give rise, not to a new fern plant, but to a leaf-like scale—the Prothallus. Upon the lower surface of this the sexual organs arise, and within them the sexual cells themselves are differentiated, and as the result of the fertilisation of one of the female cells or oospheres, by the male cell or antherozoid, a new fern plant arises. Thus in normal cases a regular alternation of a sexual with a sexless generation is seen. But although this is the course followed by the vast majority of the ferns which have been hitherto investigated, it is not the only one open to the plants. Thus Prof. Farlow in 1874 discovered that the formation of the sporophore (fern plant) generation might arise directly from the oophore (prothallus) generation, without the intervention of sexual organs, by a process resembling ordinary budding. De Bary, who followed the matter further, found that several ferns other than that examined by Farlow reproduced themselves in the same fashion, to which phenomenon the name of Apogamy was given, the marriage link being eliminated. Curiously enough De Bary found that a variety of one of our most vigorous British ferns reproduced itself constantly in this asexual manner, though the common form exhibited no abnormality in this respect. Recently, however, L. Kny,<sup>1</sup> pursuing these investigations further, has found the

<sup>1</sup> *Entwickelung von Aspidium Felix mas. Sw.*, 1 Theil., L. Kny, Berlin.

normal form to reproduce itself in both ways, and since his asexual examples occurred in thickly-sown pots, it would appear to be due to some extent to a starved condition induced by overcrowding, which checks the formation of the archegonia, and leads to the simple budding in their place. In all these instances the young plants are engendered upon precisely the same spots on the prothallus as the sexual one would occupy, and as their development and appearance are identical, it is only by preliminary watching that their apogamic origin can be determined.

A case of Apogamy (or rather two cases), however, recently occurred in a sowing of my own, which is quite distinct from any I have seen described. A sowing of a plumose variety of *Athyrium filix fæmina* failed almost entirely, only two or three prothalli surviving. One of these after growing very large, nearly half an inch across, remained perfectly dormant the whole of the summer; early in the autumn, however, the edge of the prothallus began to grow out and upwards in two places, and eventually two slightly curved horns,<sup>1</sup> each about one quarter inch long, developed perpendicularly, one on each side of the indentation or sinus common to most prothalli. Later on, at a short distance from each tip, a small whitish bulbil appeared and these increased in size until the circination of several fronds was plainly visible, a small crown or caudex being developed. No roots, however, were emitted, and the two little plants, both, be it remarked, identically situated and very like in form, were evidently supported by the prothallic root-hairs, though by this time most of the prothallus was brown and dead. Subsequently I placed a piece of loam in contact, and into this both plants rooted and fronds were sent up, the first of which had no less than ten pinnate divisions on either side. It was thus, it will be seen, very different from the usually simple primary fronds produced either sexually or apogamously heretofore. Later on still, noticing that the tips of the horns were showing signs of dilating, I cut these off with a razor and laid them

<sup>1</sup> *Gard. Chronicle*, 10th Nov., 1894.

down, two apparently normal and full-sized prothalli being the present result. In this case it will be noted that both plants were far removed from the usual site of reproduction, and both in this respect and in their vigorous development are differentiated from previously cited cases of apogamy. The second case alluded to occurred on another prothallus in the same pan, wherein the bulbil developed likewise upon a horn-like excrescence, but on the centre of the upper surface of the prothallus. This bulbil has developed into what is so far a very weakly plant of a different type to the others, but otherwise presenting no special feature.

Until 1884 the Prothallus had always been regarded as necessarily the offspring of the spore, but in the autumn of 1883 a presumed barren variety of *Athyrium filix fœmina* (*var. Clarissima*) was sent me for examination. For twenty years this plant had been observed to produce an immense number of apparent sori, but no spores were ripened or shed, and no offspring had consequently been raised. Some previous observations on dorsal bulbils, *i.e.*, bulbils associated with the spore heaps in this same species, led me to the opinion that these apparent sori, which consisted of green pear-shaped masses instead of the capsules proper to spores, did not represent bulbils, but some abnormality in the development of the sporangia. To test this I laid down portions of the fronds, and to my intense surprise these pearshaped bodies commenced at once to grow into prothalli, their tips dilating and spreading, while root-hairs and subsequently both archegonia and antheridia appeared in abundance. I at once gave a note of my observations at the Linnean Society<sup>1</sup> as demonstrating the development of the prothallus without the agency of the spore. The following season, pursuing my culture, I was able to exhibit a number of plants and such material as satisfied the society of the facts put forward.<sup>2</sup> Prof. F. O. Bower<sup>3</sup> then undertook

<sup>1</sup> "Observations on a Singular Mode of Development in the Lady Fern (*Athyrium filix fœmina*)," *Linn. Soc. Journal Botany*, vol xxi., p. 354-7.

<sup>2</sup> "Further notes on ditto," *ibid.*, vol. xxi., pp. 358-60.

<sup>3</sup> "On Apospory in Ferns (with special reference to Mr. Charles T. Druery's observations)," F. O. Bower, *ibid.*, vol. xxi., pp. 360-68.

the further investigation of the case, and found that the development of the sorus or spore heap went as far as the formation of the stalk of the sporangium or spore capsule, but at that stage it stopped and a vegetative growth set in to form the clusters of pear or club-shaped bodies which eventually went through the normal evolution of prothalli and sexual plants. Mr. G. B. Wollaston followed by providing material from a variety of *Polystichum angulare* in his possession, wherein the elimination of the spore and the entire soral apparatus was so complete that the prothalli were developed from the slender-pointed tips of the ultimate divisions of the fern-frond. Padley, *P. ang. var pulcherrimum* was the plant in question, and as it chanced that several other varieties of the same type existed, though found at widely sundered spots in England, it resulted that Dr. F. W. Stansfield and myself found the same character in two of them. Prof. Bower further observed that soral apospory, *i.e.*, the form first noted, was also present on Padley's plants, and this too we, Dr. Stansfield and myself, confirmed in the others. We have in these four examples, and in the genus *Polystichum* especially, ample proof that the spore is not an essential preliminary to the existence of the Prothallus, but that the latter may be developed direct from the tissues of the Sporophore, precisely as this latter in Apogamy may be developed direct from those of the oophore.<sup>1</sup> Curiously enough the next case which came before the writer's notice was an aposporous seedling of the same variety of *Lastrea* (*Aspidium*) determined by De Bary as being persistently apogamous, *viz.*, *Lastrea pseudo mas var. cristata*. This case was distinct from previous ones as it was a young plant and not an adult, which produced the prothalli. The tip of the second frond evolved from the prothallus (the first was eaten off and was not seen) bore a prothallus of the normal form. Subsequently this and the succeeding

<sup>1</sup> Professor F. O. Bower subsequently prepared an exhaustive monograph "On Apospory and Allied Phenomena". *Linnean Transactions*, vol. ii., part 14, July, 1887, to which reference should be made for details of the preceding cases.

frond became covered with prothalli developed not merely from the edges, but also from the upper surface, and being pegged down produced a number of plants, but whether apogamously or not I cannot say, though from De Bary's observations, they should be so. It is worthy of remark that in some of these youngsters, the line between the two generations of sporophore and oophore was so vague that the primary fronds were simply stalked prothalli, the next frond half one and half the other, while the fourth or fifth had quite outgrown the tendency and were of the typical varietal form. This plant was exhibited and described at the Linnean Society, 3rd November, 1892.<sup>1</sup> Of the next two cases I observed, the first was an *Athyrium* found in Lancashire and exhibited in 1893 at the meeting of the Pteridological Society at Lancaster by Mr. Bolton the finder. Immediately on seeing it I remarked, "How very like Col. Jones's *Clarissima*," simultaneously with which Mr. Bolton said, "It is strange, but it never ripens its spores". Turning the frond over, the reason was clear, it was perfectly white with aposporal excrescences. On submitting these to culture they produce plants freely by sexual action, but of two types, one very depauperate, mere skeleton plants, and the other of the parental form with occasional reversion towards the normal. In some of these young plants the whitish excrescences are plentiful in fronds only an inch or two high, and there are evident signs of prothalloid growth at the tips of the segments as well, pointing to apical apospory when the plants are more developed. The next case occurs in a most unlikely species, especially as apical apospory is in question. This is seen in a variety of *Scolopendrium vulgare* (*S. v. crispum Drummondii*) which occurs in the wild state, like all the rest, characterised by being frilled and crested, and having moreover a finely fimbriated edge to the fronds. Visiting Mr. Bolton to inspect the *Athyrium* last cited, I saw a fine plant of this fern, and it immediately struck me that the tips of

<sup>1</sup>"Notes on an Aposporous *Lastrea* (*Nephrodium*)" *Linn. Soc. Journal Botany*, vol. xxix., pp. 479-82.

the fimbriate projections were remarkably translucent. I obtained material, laid it down, and at once prothalli began to develop vigorously from every point, so vigorously indeed that a single tip has formed a mass of prothalli an inch across which yielded at least a dozen plants of the parental form.<sup>1</sup>

Dr. F. W. Stansfield has recently sent me prothalli developed from a finely fimbriated form of *Lastrea* of which the reputed parent is that already described, and informs me that it is profusely aposporous though fairly developed in size.

By the various instances of this phenomenon so far cited, we see that the normal life cycles of the ferns in question have been successively shortened, first by the elision of the spore and then by that of the whole soral apparatus, while if we accept De Bary's observations as establishing the constant apogamous reproduction of *L. pseudo mas cristata*, in that case, it is shortened almost to the utmost, the chain being simply sporophore, prothallus, sporophore. Consistently indeed with the alternation of generation the chain could not apparently be shorter since the prothallus being eliminated we naturally come, or seem to come, to simple bulbils, such as occur on many ferns, *Asplenium bulbiferum* for example. In the final case, however, which I have to cite, we arrive at the elimination even of the prothallus by substitution of the frond itself as the oophore or egg-bearer, the archegonia and antheridia being generated upon the frond without the prior formation of a prothallus proper. In a small plant of *Scolopendrium vulgare* recently sent me by Mr. E. J. Lowe, and exhibited by me at the Linnean Society in November last, although a definite axis of growth had been formed and several fronds had arisen in the normal spiral fashion around it, indicating that the prothallus stage had been unmistakeably passed, each of these fronds bore a thickened cushion at its tip upon which were seated both

<sup>1</sup>"Note on Apospory in a form of *Scolopendrium vulgare*," etc., *Linn. Soc. Journal*, vol. xxx., pp. 281-84.

antheridia and archegonia, accompanied by aerial roothairs, the frond itself thus assuming the functions of the prothallus. Mr. Lowe raised a number of similar plants on the genesis of which he is preparing a paper which I will not forestall; but he informs me that in time they throw off this aposporous character. Fronds which he has sent me, and which I have laid down, have developed prothalli all over their surface and at all terminals, but so far my cultures are too recent to permit me to report the advent of plants.

This completes the sketch of the cases which have come under my immediate notice, but considering that, including the first discovery, the phenomenon has been observed in no less than nine instances in our limited number of British species, *viz.*, *Lastrea (Nephrodium)* two, *Athyrium filix fœmina* two, *Polystichum angulare* three, and *Scolopendrium vulgare* two; it is only reasonable to expect that many undiscovered instances must occur in the innumerable other species existent throughout the world.

CHARLES T. DRUERY.